Social Mongoose Vocal Communication: Insights into the Emergence of Linguistic Combinatoriality

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CONTENT:

SUMMARY:

Duality of patterning, language's ability to combine sounds on two levels, phonology and syntax, is considered one of human language's defining features, yet relatively little is known about its origins. One way to investigate this is to take a comparative approach, contrasting combinatoriality in animal vocal communication systems with phonology and syntax in human language. In my thesis, I took a comparative approach to the evolution of combinatoriality, carrying out both theoretical and empirical research. In the theoretical domain, I identified some prevalent misunderstandings in research on the emergence of combinatoriality that have propagated across disciplines. To address these misconceptions, I re-analysed existing examples of animal call combinations implementing insights from linguistics. Specifically, I showed that syntax-like combinations are more widespread in animal communication than phonology-like sequences, which, combined with the absence of phonology in some human languages, suggested that syntax may have evolved before phonology. Building on this theoretical work, I empirically explored call combinations in two species of social mongooses. I first investigated social call combinations in meerkats (*Suricata suricatta*), demonstrating that call combinations represented a non-negligible component of the meerkat vocal communication system and could be used flexibly across various social contexts. Furthermore, I discussed a variety of mechanisms by which these combinations could be produced. Second, I considered call combinations in predation contexts. In particular, I investigated dwarf mongoose (*Helogale parvula*) alarm call combinations. To do so, I documented their alarm call repertoire, showing that they emitted multiple different alarm calls, of which some were risk related and some were more predator specific. The function of the last, rarely produced, alarm calls remained ambiguous. I then demonstrated that the dwarf mongoose "type 3" (hereafter T_3) alarm call represented a combination of their predator specific aerial and terrestrial alarm calls. Observational and experimental data suggested that T_3 was a general alarm call with a possible meaning akin to "(aerial or terrestrial) predator". From a linguistic perspective this combination could be interpreted as a rudimentary form of disjunction, with disjunction being a form of syntax that combines two or more units in which at least one of the propositions is true, but not necessarily both (e.g. "*he is right **or** wrong"*). To my knowledge, this would represent the first evidence for this type of combination outside of human language. The data obtained in this thesis showed that social mongooses used call combinations in all facets of their communication, from social to anti-predator situations, and indicated that both of these contexts may play a role in the evolution of combinatoriality. Furthermore, some of the combinations described in this thesis seemed to be the result of simple mechanisms far removed from the combinatoriality seen in human language, whereas others appeared to be rudimentary forms of syntax. Nevertheless, studying combinatoriality across several species' communication systems can help not only identify the similarities and differences between animal call combinations and linguistic forms of combinatoriality but also, ultimately, help elucidate the impact of different factors, both social and environmental, on the evolution of combinatoriality.

ZUSAMMENFASSUNG:

Die Fähigkeit Laute auf zwei Ebenen, Phonologie und Syntax, zu kombinieren, wird als eine Haupteigenschaft der menschlichen Sprache angesehen. Dennoch ist über den Ursprung dieser kombinatorischen Strukturen – auch Kombinatorialität genannt, relativ wenig bekannt. Eine Möglichkeit dies zu erforschen besteht darin, einen vergleichenden Ansatz zu wählen und dabei Kombinationen in den Kommunikationssystemen verschiedenster Tiere mit jenen des phonologischen und syntaktischen Systems der menschlichen Sprache zu vergleichen. In meiner Dissertation habe ich diesen vergleichenden Ansatz angewandt, um die Evolution von Kombinatorialität, sowohl auf theoretischer wie auch auf empirischer Ebene, besser zu verstehen. Auf theoretischer Ebene habe ich zunächst zu weit verbreiteten Missverständnissen bezüglich der Evolution von Kombinatorialität Stellung genommen. Um diese teils falsch verstandenen Auffassungen und Vorstellungen zu berichtigen, habe ich Ansätze aus der Linguistik verwendet, um bereits bestehende Beispiele von Kombinatorialität in tierischen Kommunikationssystemen neu zu analysieren. Dabei konnte ich zeigen, dass in tierischen Kommunikationssystemen Kombinationen auf der Ebene von Syntax weiter verbreitet sind als phonologische Kombinationen. Zusammen mit der Abwesenheit von Phonologie in einigen menschlichen Spachen wies dies darauf hin, dass sich Syntax sehr wahrscheinlich vor Phonologie entwickelt hat. Basierend auf diesem theoretischen Hintergrund habe ich anschließend Rufaufnahmen von zwei Arten sozial lebender Mangusten auf das Vorkommen von Rufkombinationen hin untersucht. Zuerst habe ich Rufkombinationen in Erdmännchen (*Suricata suricatta*), welche hauptsächlich in sozialen Zusammenhängen produziert werden, analysiert und dabei herausgefunden, dass Rufkombinationen einen erheblichen Anteil des Kommunikationssystem der Erdmännchen ausmachen, und in verschiedenen Situationen flexibel gebraucht werden. Des Weiteren habe ich eine Auswahl von Mechanismen diskutiert, welche zur Produktion dieser Rufkombinationen führen könnten. Um ein möglichst vollständiges Bild zur Verwendung von Rufkombinationen in sozial lebenden Mongusten zu erhalten, habe ich zusätzlich zu den Rufkombinationen aus sozialen Kontexten noch diejenigen aus Räuberkontexten in Betracht gezogen. Dazu, habe ich Rufkombinationen bei Zwergmangusten (*Helogale parvula*) untersucht. Ich habe das gesamte Repertoire von Alarmrufen dokumentiert und gezeigt, dass Zwergmangusten eine Vielzahl von verschiedenen Alarmrufen produzieren, von welchen einige Informationen zur Dringlichkeit einer Fluchtreaktion der Gruppe enthalten, während andere Alarmrufe Informationen über die Art des Räubers beinhalten. Die Funktion einiger seltener produzierter Alarmrufe konnte nicht mit voller Gewissheit bestimmt werden. Ich konnte zeigen, dass der Zwergmangusten Alarmruf „Typ 3“ (nachstehend T_3 genannt) eine Kombination der beiden Alarmrufe für Feinde aus der Luft (Lufträuber) und Feinde vom Boden (Bodenräuber) darstellt. Daten aus natürlichen Beobachtungen, sowie aus experimentellen Versuchen wiesen darauf hin, dass T_3 eine eher generelle Bedeutung hat, welche auf Bodenräuber oder Räuber aus der Luft hinweist. Von einem linguistischen Standpunkt aus, kann dieser T_3 Alarmruf als eine ursprüngliche Form einer Disjunktion interpretiert werden. Disjunktionen beschreiben eine Form von Syntax, bei welcher zwei oder mehr Aussagen durch ein ‚oder' miteinander verknüpft sind und von denen mindestens

eine wahr ist (z.B. „*Er liegt richtig **oder** falsch*“). Meines Wissens ist dies der erste Nachweis dieser Art von Kombination ausserhalb der menschlichen Sprache. Die Daten, welche während dieser Dissertation erhoben wurden, haben gezeigt, dass sozial lebende Mangusten eine Vielzahl von Rufkombination in verschiedenen Bereichen ihrer Kommunikation, von sozialen bis Räuber-Beute-Zusammenhängen, nutzen, und dass wahrscheinlich beide Kontexte in der Entstehung von Kombinatorialität eine wichtige Rolle gespielt haben. Zudem scheint es so, dass einige der Kombinationen so wie sie in dieser Dissertation beschrieben wurden, vielmehr das Resultat von einfachen Mechanismen darstellen und nicht mit Kombinatorialität, wie wir es in der menschlichen Sprache finden, verglichen werden können. Andere Kombinationen, die ich gefunden habe, scheinen jedoch ursprüngliche Formen von Syntax zu verkörpern. Abschließend kann der Vergleich von Kombinatorialität im Kommunikationssystem verschiedener Tierarten helfen, Ähnlichkeiten sowie auch Unterschiede zwischen Rufkombinationen bei Tieren und linguistischen Formen von Kombinatorialität in der menschlichen Sprache zu finden. Zu guter Letzt kann dies helfen, den Einfluss verschiedener ökologischer sowie sozialer Faktoren auf die Entstehung von Kombinatorialität besser zu verstehen.

GENERAL INTRODUCTION:

Language has fascinated philosophers and scientists alike since early Antiquity (Aristotle, 350AD). Deemed one of humans' unique and distinguishing features, language promotes the transfer of knowledge between individuals and generations (Nowak, 2000), which in turn plays a key role in other defining facets of humanity such as culture for example (Fitch, 2011). For this reason the emergence of language is considered a major evolutionary transition (Szathmáry and Maynard Smith, 1995). Yet, despite its importance for humans, little is currently known about how language evolved.

One of the main barriers to the study of the origins of language is that it does not leave any direct traces of its presence and so researchers must find ways to circumvent this problem. The study of child language acquisition (Tomasello, 2003), hominid morphology (Lieberman, 1973, 1984, 1998), genetics (Enard et al., 2002) and the use of computer simulations (Deacon, 2003; Kirby, 2001; Nowak and Komarova, 2001) are among some of the methods used to explore the evolution of language. However, investigating the evolution of language as a whole, undividable unit is non-trivial and requires decomposing language down into its various components and examining their origins separately. The American linguist Charles F. Hockett (1960) was one of the first to take such an approach, dividing language into 13 design features (table 1), present in all spoken languages, to facilitate comparisons with other communication systems. One of these design features which has received particular interest is duality of patterning (Hockett, 1960), also known as double articulation (Martinet, 1949). Duality of patterning is the linguistic phenomenon where sounds are combined on two distinct levels (Hockett, 1960). On the first level, phonology, meaningless sounds termed phonemes are combined into meaningful words or morphemes (McGregor, 2009). Whilst phonemes are meaningless in themselves, they play an important role in differentiating the meanings of the words they compose (Hockett, 1960), either by their order within the word (e.g. "*cat*" vs "*act*") or by their presence or absence (e.g. "*at*" vs "*cat*"). On a second, syntactic level, meaningful sounds, words or morphemes, are combined into larger meaningful structures whose meaning is derived from the meaning of their parts (McGregor, 2009). Duality of patterning, highlighted as a 'fundamental universal structural characteristic' of language (Hurford, 2002), is commonly regarded as the primary facilitator behind language's productivity, the capacity to create infinite messages from finite means (von Humboldt, 1999). A better understanding of how duality of patterning evolved could offer insights into the evolution of language as a whole.

Scientists from various fields have approached the question of the origins of duality of patterning in different, though complementary, ways. Linguists have, for example, examined

Table 1: Hockett's design-features of language (Hockett, 1960).

Design feature	Description
Vocal-auditory channel (only for spoken languages)	The signal is transmitted as a sound on the vocal channel and received on the auditory channel
Broadcast emission and directional reception	Signal is emitted in all directions whereas the receiver can pinpoint the origin of the signal by binaural direction-finding
Rapid fading (transitoriness)	The signal does not linger, it is available for the receiver only for a very short period of time
Interchangeability	An individual can receive all the signals it emits and vice versa
Total feedback (only for spoken languages)	The emitter also receives (hears) the signal it is emitting
Specialization	Signals only function as signals and are not used for any other purpose
Semanticity	Fixed association between a signal and an external event
Arbitrariness	There is no relation between the object designated and the physical structure of the signal
Discreteness	Signals are perceived as discrete (as opposed to graded or continuous)
Displacement	Ability to refer to something distant in time or space
Productivity	Ability to produce signals that have never been produced before and be understood
Cultural transmission	Conventions of language use are transmitted from one individual to another extra-genetically
Duality of patterning	Ability to combine sounds on two levels: - Phonology: meaningless sounds, phonemes, into meaningful words - Syntax: meaningful words into larger meaningful structures

the emergence of syntax during child language acquisition (De Villiers and De Villiers, 1978; Miller and Chapman, 1981) or investigated the development of phonology and syntax in newly emerging languages. Regarding newly emerging languages, given that the vast majority of modern humans are exposed to and learn a developed language from early childhood, these

studies have focused on deaf communities for which there is no initial linguistic input (Goldin-Meadow and Feldman, 1977). Two emerging languages that have been the target of such research are the Nicaraguan Sign Language (Senghas et al., 2004; Senghas and Coppola, 2001) and the Al-Sayyid Bedouin Sign Language (Sandler et al., 2011, 2014). Furthermore, computational linguistics, in which language development within a simulated population of individuals that behave according to defined rules is observed, can be used to explore the emergence of combinatoriality (Kirby, 2000).

Animal biologists have also shown an interest in the evolution of combinatoriality. Here, researchers mainly take a comparative approach to the study of duality of patterning, looking for similar features to phonology and syntax in animal communication systems. If similar features are found in species closely related to humans, such as non-human primates for example, they are likely homologues, inherited features from a common ancestor and can provide insight into the phylogenetic origins of this trait. However, if similar features are found in species more distantly related to humans, then they possibly evolved independently. In this case, such features are termed analogues and have the advantage of potentially informing on the social or environmental factors that favoured their emergence. In order to facilitate the comparison between human and animal vocal combinations, Peter Marler (1998) coined several terms to describe sound combinations in animal communication. Loosely based on the levels of duality of patterning, these terms include phonological syntax or phonocoding and lexical syntax or lexicoding (Marler, 1998). Phonological syntax describes a combination of meaningless sounds into larger units whereas lexical syntax describes a combination of meaningful sounds into a structure whose meaning reflects the meaning of its parts (Marler, 1998). Whilst phonological syntax is recognised in some animal communication systems, in particular in bird- and whale-song, lexical syntax has long been thought to be rare or perhaps even absent outside of human language (Hurford, 2011). However, some recent studies suggest that some animal species, including primates and birds, do combine meaningful calls into larger meaningful sequences (Engesser et al., 2016; Ouattara et al., 2009; Suzuki et al., 2016).

Despite the question of language evolution encompassing a variety of disciplines, there is a surprising lack of communication amongst them. This is problematic as it can lead to misconceptions that are counterproductive to advances in the field. For example, due to the similarity between the terms ‘phonology’ and ‘phonological syntax’, it is often assumed by animal biologists that the combinatoriality seen in birdsong is the same as phonology in human language (Yip, 2006). There are however some important differences between the phonological

syntax seen in birdsong and linguistic phonology; whilst birdsong and human words are both composed of meaningless sounds, changing the order of sounds in a word affects its meaning whereas, for many species, rearranging the notes within a birdsong does not change the message conveyed (Hurford, 2011; Marler, 1998). A similar issue arises with the term 'syntax'. Whilst in linguistics it defines a specific type of combination of meaningful sounds, in animal communication it is often incorrectly used to refer to the temporal patterning of sound units within sequences such as bird- (Marler and Slabbekoorn, 2004; Bregman and Gentner, 2010), whale- (Payne and McVay, 1971) and bat-song (Bohn et al., 2013).

An increase in interdisciplinary studies on the evolution of combinatoriality is therefore crucial in order to broaden exchanges between disciplines. This would help reduce misinterpretations and avoid unnecessary controversies, thus contributing considerably to advances in the field. The comparative approach in particular could benefit greatly from interdisciplinary research, with linguistic analyses of animal call combinations helping to facilitate accurate comparisons with combinatoriality in human language, for example.

Thesis Aims

With this thesis, I aimed to take an interdisciplinary approach to better understand the evolutionary emergence of combinatoriality in vocal communication systems. Benefitting from inputs from the fields of animal science, linguistics and anthropology, I carried out both theoretical and empirical research. The theoretical dimension addressed some common misconceptions between fields by comparing terminology for combinatoriality used in animal communication and linguistics. Furthermore, I re-analysed several animal call combinations described in the literature from a linguistic perspective. This facilitated comparisons between the different forms of animal vocal combinations documented and the two levels of duality of patterning in human language, potentially leading to new insights on the emergence of combinatoriality.

The empirical work of this thesis built on developments arising from the theoretical study and examined the extent and use of call combinations in two species of cooperative breeding mongooses, meerkats (*Suricata suricatta*) and dwarf mongooses (*Helogale parvula*). Studying call combinations in two species of comparable size and social structure and that face similar predation threats but live in different habitats is one way to begin to disentangle the relative contribution of social and ecological factors on the production of combinations. Additionally,

previous research has documented call combinations within this taxon (banded mongooses, *Mungos mungo*: Jansen et al., 2012; meerkats: Manser et al., 2014), but to date these combinations have not been the focus of any systematic studies.

Social mongooses are particularly interesting to study in the context of the emergence of combinatoriality because they are both highly vocal and highly social and may therefore rely on vocalisations to coordinate different behaviours and interactions including social interactions, spatial coordination and anti-predator behaviours (Manser et al., 2014). However, most terrestrial mammals' vocal repertoires are constrained in the number of calls they can produce (Seyfarth and Cheney, 2010) which could lead to the production of call combinations if there are more behaviours to coordinate than calls available in the repertoire (Nowak and Krakauer, 1999; Arnold and Zuberbühler, 2006). Social contexts, in which there is a large diversity of behaviours, may therefore be particularly fruitful situations in which to search for combinations. Moreover, in most social contexts an immediate response is not as critical to survival as in predation contexts, potentially giving callers and receivers time to produce and process longer call combinations. Nevertheless, most studies on call combinations outside of vocal-learners have focused on predation contexts, leading to a lack of data on combinatoriality in non-dangerous contexts (though see Crockford & Boesch, 2005 and Bouchet et al., 2010). Consequently, I systematically documented social call combinations produced by meerkats.

However, in order to gain an overall view of combinatoriality in social mongooses, predation contexts cannot be neglected, particularly as most combinations of meaningful calls described to date have been documented in predation situations. These combinations are of specific interest because they are the most likely to be similar to syntax in human language. As previous research suggested that dwarf mongooses possessed an unusually complex alarm call system (Beynon and Rasa, 1989), I investigated their alarm call repertoire and any combinations of these calls they may produce.

Whilst recent studies have described call combinations in several animal species, to date, few have implemented an explicitly linguistic approach as a way to probe their implications for understanding language evolution. A systematic search for and linguistic analysis of call combinations across a species' repertoire is the next step to understanding the evolution of combinatoriality. By taking a comparative approach focussing on species more distantly related to humans than our primate cousins, I aimed to investigate environmental or social factors that could favour the emergence of call combinations.

Figure 1: Adult meerkat vigilant in a bipedal position.

Study Species and Study Sites

*Meerkats (*Suricata suricatta*)*

Meerkats are small social mongooses weighing between 600 and 800g (figure 1; Manser et al., 2014). They live in arid or semi-arid habitats (Doolan and Macdonald, 1996) and form groups of up to 50 individuals, composed of one dominant pair and several subordinate adults, juveniles and pups (Clutton-Brock et al., 2006). Reproduction is generally limited to the dominant pair and all members of the group help rear the pups (Clutton-Brock et al., 1999b). Meerkats forage for small prey items such as insects and small vertebrates as part of a cohesive group (Doolan and Macdonald, 1996). They are subject to high predation pressures (Clutton-Brock et al., 1999a) and, while foraging, one member of the group often goes on sentinel, scanning for predators from an elevated position (Clutton-Brock et al., 1999c). Meerkats on sentinel emit several different call types in the absence of predators (Manser, 1999) and alarm calls when a predator is detected (Clutton-Brock et al., 1999c). Meerkats are highly vocal, producing over 30 different call types in contexts such as affiliative and agonistic social

interactions (e.g. grooming, submission, aggression), babysitting, spatial coordination, sunning behaviour, sentinel behaviour and anti-predator behaviour (Manser, 1998; Manser et al., 2014). Study populations were habituated to close observations by human experimenters and allowed recordings within 0.5-3m. All individuals had a transponder as part of long term data collection for the Kalahari Meerkat project (KMP) and were marked with small dye patches for field identification.

Research on this species was carried out at the KMP situated in the Northern Cape region of South Africa (26°58'S, 21°49'E) (figure 2). This semi-desertic area is comprised of the dry river bed of the Kuruman surrounded by thinly vegetated sand dunes (Clutton-Brock et al., 1998). Average annual rainfall is around 250mm (Clutton-Brock et al., 1998).

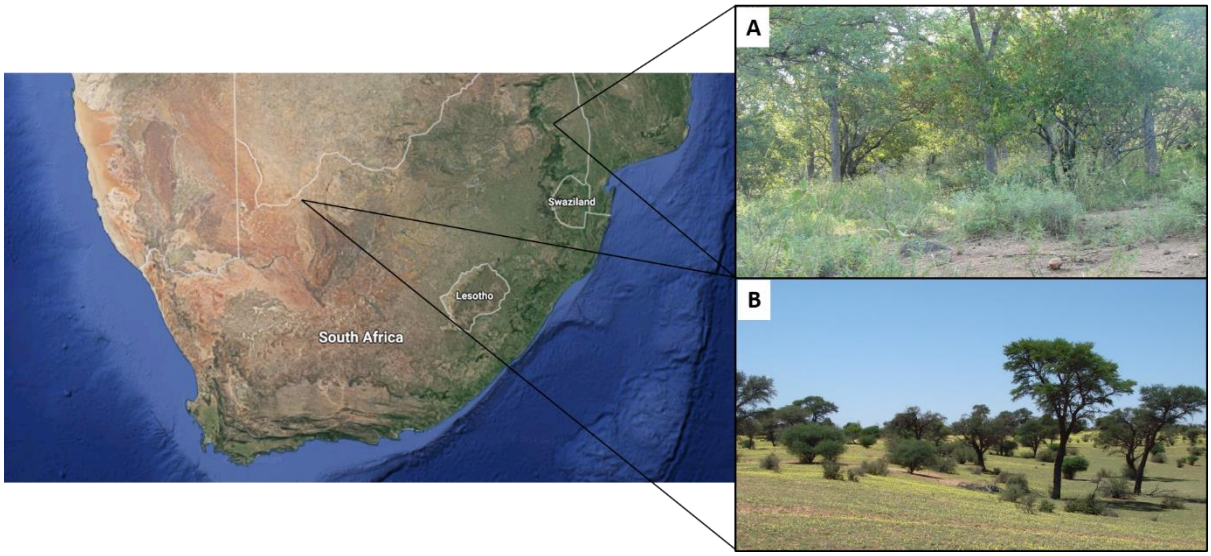

Figure 2: Location of study sites at which research for this thesis was carried out. Enlarged frames show an example the habitat and vegetation at the sites. A) Sorabi Rock Lodge Reserve and B) Kalahari Meerkat Project.

*Dwarf mongooses (*Helogale parvula*)*

Dwarf mongooses are small (up to 280g; Sharpe et al., 2010), social mongooses (figure 3). They are found in African woodlands and wooded savannas and live in groups of up to 30 individuals (Rasa, 1977). These groups are composed of a dominant pair, their offspring of the year and several subordinate mongooses of both sexes that can be either related individuals or unrelated immigrants (Keane et al., 1994). Dwarf mongooses are cooperative breeders with

reproduction generally monopolised by the dominant pair and the rest of the group participating in raising pups to maturity (Keane et al., 1994). Dwarf mongooses' small size leaves them vulnerable to a wide range of aerial and terrestrial predators. During foraging one individual often engages in sentinel behaviour, vigilance in an elevated position, whilst the rest of the group forages (Rasa, 1986). The sentinel alerts the rest of the group to the presence of danger by alarm calling (Rasa, 1986). All studied mongooses were habituated to the presence of human observers and could be recorded from a close distance (<5 m). Individuals could be distinguished thanks to small dye-marks or individual features such as scars.

Research on this species took place at Sorabi Rock Lodge Reserve, a private game reserve in the Limpopo province of South Africa (24°11'S, 30°46'E) (figure 2; Kern and Radford, 2013). This area is part of the Lowveld climate with cold dry winter (May-August) and hot rainy summers (September-April) (Kern and Radford, 2013). Potential dwarf mongoose predators present on the site are shown in figure 4 (Kern and Radford, 2014).

Figure 3: Two adult dwarf mongooses vigilant on a rock.

Thesis Outline

Chapter 1 begins with a theoretical approach, reviewing examples of call combinations in animal communication from the literature. In this chapter, I evaluate how these combinations compare to the two layers of combinatoriality in human language, phonology and syntax. I also present relevant examples from human languages, both spoken and signed. With input from researchers from different fields (biology, linguistics, anthropology), I then discuss their implications on the evolutionary origins of phonology and syntax.

In **chapter 2**, I take an observational empirical approach to investigating social call combinations in meerkats. I systematically document all combinations produced by meerkats in various social contexts and discuss their role in communication and the mechanisms by which they may be produced. Furthermore, I compare these social combinations to meerkat call combinations produced in predation contexts as described in previous work and consider the significance of the results in relation to the emergence of combinatoriality.

The last two chapters also follow an empirical approach, however here the naturalistic observations are complemented by experimental work. In these chapters, I explore dwarf mongoose alarm call combinations. In order to do so, I first describe their alarm call system in **chapter 3**. In **chapter 4**, I then investigate whether dwarf mongooses do indeed combine their aerial and terrestrial calls into a third alarm call. In order to avoid an erroneous interpretation of this call combination, I take a linguistic analysis approach and propose multiple interpretations and their likelihood of being correct in relation to the data collected. I then discuss where dwarf mongoose alarm calls fit in the framework of known call combinations in animal communication.

Finally, in the **general discussion**, I summarize what is known about call combinations in social mongooses and consider its implications for the evolution of combinatoriality in human languages. Furthermore, I present several methodological issues with the comparative approach and offer some possible solutions. A future research direction, highlighted in the outlook section, could be to investigate dwarf mongoose social call combinations.

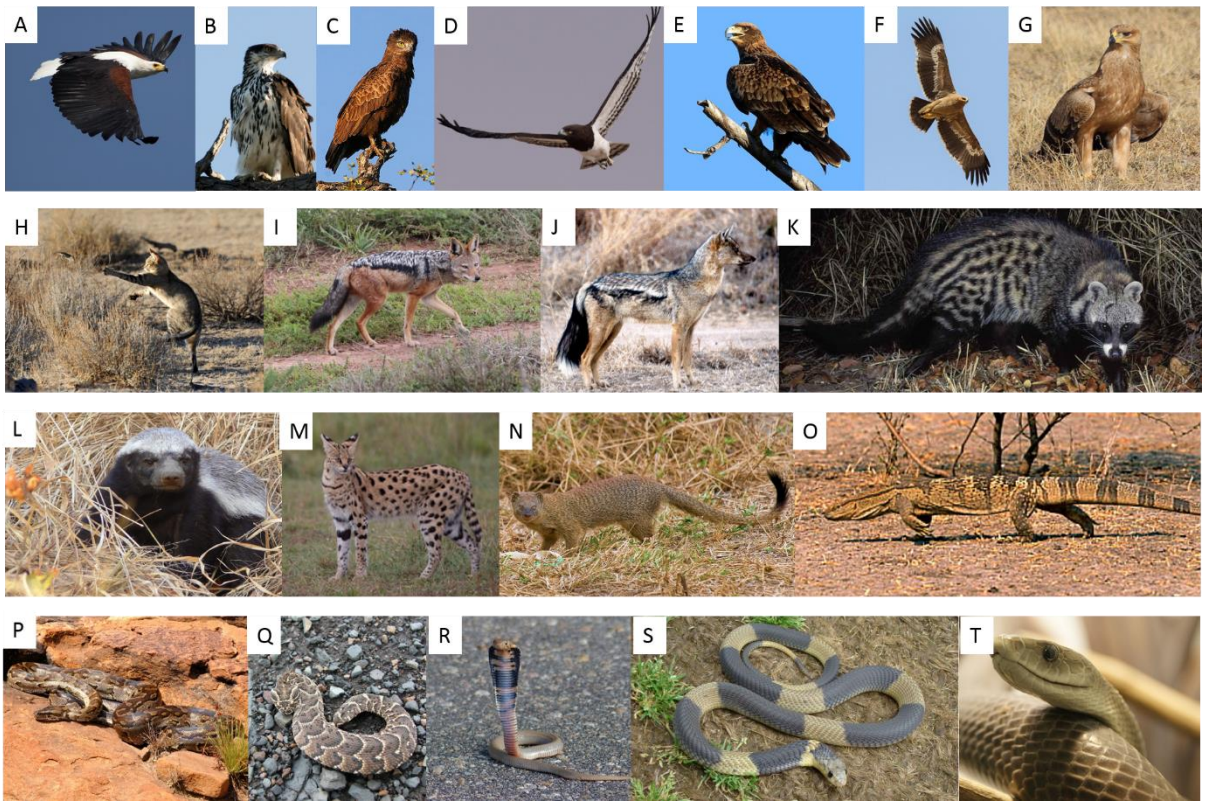

Figure 4: Potential dwarf mongoose predators present at the study site. Aerial predators: A) African fish-eagle (*Haliaeetus vocifer*), B) African hawk-eagle (*Hieraaetus spilogaster*), C) brown snake-eagle (*Circaetus cinereus*), D) blackbreasted snake-eagle (*Circaetus pectoralis*), E) tawny eagle (*Aquila rapax*), F) steppe eagle (*Aquila nipalensis*), G) Wahlberg's eagle (*Aquila wahlbergi*); Quadrupedal terrestrial predators: H) African wildcat (*Felis lybica*), I) black-backed jackal (*Canis mesomelas*), J) side-striped jackal (*Canis adustus*), K) African civet (*Civettictis civetta*), L) honey badger (*Mellivora capensis*), M) serval (*Felis serval*), N) slender mongoose (*Galerella sanguinea*), O) rock monitor (*Varanus exanthematicus*); Snakes: P) African rock python (*Python sebae*), Q) puff adder (*Bitis arietans*), R) Mozambique spitting cobra (*Naja mossambica*), S) snouted cobra (*Naja haje*) and T) black mamba (*Dendroaspis polylepis*).

REFERENCES

Aristotle, 350AD. The History of Animals. Kessinger Publishing, Whitefish, Montana, USA.

Arnold, K., Zuberbühler, K., 2006. Language evolution: Semantic combinations in primate calls. Nature 441, 303–303. doi:10.1038/441303a

Beynon, P., Rasa, O.A.E., 1989. Do dwarf mongooses have a language?: Warning vocalisations transmit complex information. South Afr. J. Sci. 85, 447–450.

Bohn, K.M., Smarsh, G.C., Smotherman, M., 2013. Social context evokes rapid changes in bat song syntax. Anim. Behav. 85, 1485–1491. doi:10.1016/j.anbehav.2013.04.002

Bouchet, H., Pellier, A.-S., Blois-Heulin, C., Lemasson, A., 2010. Sex differences in the vocal repertoire of adult red-capped mangabeys (*Cercocebus torquatus*): a multi-level acoustic analysis. Am. J. Primatol. 72, 360–375. doi:10.1002/ajp.20791

Bregman, M.R., Gentner, T.Q., 2010. Syntactically complex vocal systems, in: Breed, M.D., Moore, J. (Eds.), Encyclopedia of Animal Behavior. pp. 368–374.

Clutton-Brock, T.H., Gaynor, D., Kansky, R., MacColl, A.D.C., McIlrath, G.M., Chadwick, P., Brotherton, P.N.M., O'Riain, J.M., Manser, M.B., Skinner, J.D., 1998. Costs of cooperative behaviour in suricates (*Suricata suricatta*). Proc. R. Soc. B Biol. Sci. 265, 185–190. doi:10.1098/rspb.1998.0281

Clutton-Brock, T.H., Gaynor, D., McIlrath, G.M., Maccoll, A.D.C., Kansky, R., Chadwick, P., Manser, M.B., Skinner, J.D., Brotherton, P.N.M., 1999a. Predation, group size and mortality in a cooperative mongoose, *Suricata suricatta*. J. Anim. Ecol. 68, 672–683.

Clutton-Brock, T.H., Hodge, S.J., Spong, G., Russell, A.F., Jordan, N.R., Bennett, N.C., Sharpe, L.L., Manser, M.B., 2006. Intrasexual competition and sexual selection in cooperative mammals. Nature 444, 1065–1068. doi:10.1038/nature05386

Clutton-Brock, T.H., Maccoll, A., Chadwick, P., Gaynor, D., Kansky, R., Skinner, J.D., 1999b. Reproduction and survival of suricates (*Suricata suricatta*) in the southern Kalahari. Afr. J. Ecol. 37, 69–80. doi:10.1046/j.1365-2028.1999.00160.x

Clutton-Brock, T.H., O'Riain, M.J., Brotherton, P.N.M., Gaynor, D., Kansky, R., Griffin, A.S., Manser, M.B., 1999c. Selfish sentinels in cooperative mammals. Science 284, 1640–1644. doi:10.1126/science.284.5420.1640

Crockford, C., Boesch, C., 2005. Call combinations in wild chimpanzees. Behaviour 142, 397–421. doi:10.1163/1568539054012047

De Villiers, J.G., De Villiers, P.A., 1978. Language acquisition. Harvard University Press.

Deacon, T.W., 2003. Universal grammar and semiotic constraints, in: Christiansen, M.H., Kirby, S. (Eds.), Language Evolution. Oxford University Press, Oxford, UK, pp. 111–139.

Doolan, S.P., Macdonald, D.W., 1996. Diet and foraging behaviour of group-living meerkats, *Suricata suricatta*, in the southern Kalahari. J. Zool. 239, 697–716. doi:10.1111/j.1469-7998.1996.tb05472.x

Enard, W., Przeworski, M., Fischer, S.E., Lai, C.S., Wiebe, V., Kitano, T., Monaco, A.P., Pääbo, S., 2002. Molecular evolution of FOXP2, a gene involved in speech and language. Nature 418, 869–872.

Engesser, S., Ridley, A.R., Townsend, S.W., 2016. Meaningful call combinations and compositional processing in the southern pied babbler. Proc. Natl. Acad. Sci. 201600970.

Fitch, W.T., 2011. Unity and diversity in human language. Philos. Trans. R. Soc. B Biol. Sci. 366, 376–388. doi:10.1098/rstb.2010.0223

Goldin-Meadow, S., Feldman, H., 1977. The development of language-like communication without a language model. Science 197, 401–403.

Hockett, C.F., 1960. The origin of speech. Sci. Am. 203, 88–111.

Hurford, J.R., 2011. The origins of grammar: Language in the light of evolution II. Oxford University Press, Oxford, UK.

Hurford, J.R., 2002. The roles of expression and representation in language evolution, in: Wray, A. (Ed.), The Transition to Language. Oxford University Press, Oxford, UK, pp. 311–334.

Jansen, D.A.W.A.M., Cant, M.A., Manser, M.B., 2012. Segmental concatenation of individual signatures and context cues in banded mongoose (*Mungos mungo*) close calls. BMC Biol. 10, 97. doi:10.1186/1741-7007-10-97

Keane, B., Waser, P.M., Creel, S.R., Creel, N.M., Elliott, L.F., Minchella, D.J., 1994. Subordinate reproduction in dwarf mongooses. Anim. Behav. 47, 65–75.

Kern, J.M., Radford, A.N., 2014. Sentinel dwarf mongooses, *Helogale parvula*, exhibit flexible decision making in relation to predation risk. Anim. Behav. 98, 185–192. doi:10.1016/j.anbehav.2014.10.012

Kern, J.M., Radford, A.N., 2013. Call of duty? Variation in use of the watchman's song by sentinel dwarf mongooses, *Helogale parvula*. Anim. Behav. 85, 967–975. doi:10.1016/j.anbehav.2013.02.020

Kirby, S., 2001. Spontaneous evolution of linguistic structure: an iterated learning model of the emergence of regularity and irregularity. IEEE J Evol Comput 5, 102–110.

Kirby, S., 2000. Syntax without natural selection: How compositionality emerges from vocabulary in a population of learners, in: Knight, C. (Ed.), The Evolutionary Emergence of Language: Social Function and the Origins of Linguistic Form. Cambridge University Press, Cambridge, UK, pp. 303–323.

Lieberman, P., 1998. Eve spoke; Human Language and Human Evolution. W. W. Norton, New York.

Lieberman, P., 1984. The Biology and Evolution of Language. Harvard University Press, Cambridge, Massachusetts.

Lieberman, P., 1973. On the evolution of speech, in: Anderson, S., Kiparsky, P. (Eds.), Festschrift for Morris Halle. Holt, Rinehart and Winston, New York, pp. 107–127.

Manser, M.B., 1999. Response of foraging group members to sentinel calls in suricates, *Suricata suricatta*. Proc. R. Soc. B Biol. Sci. 266, 1013–1019. doi:10.1098/rspb.1999.0737

Manser, M.B., 1998. The evolution of auditory communication in suricates, *Suricata suricatta*. (PhD). University of Cambridge, Cambridge, UK.

Manser, M.B., Jansen, D.A.W.A.M., Graw, B., Hollén, L.I., Bousquet, C.A.H., Furrer, R.D., le Roux, A., 2014. Vocal complexity in meerkats and other mongoose species, in: Advances in the Study of Behavior. Elsevier, pp. 281–310.

Marler, P., 1998. Animal communication and human language, in: Jablonski, N.G., Aiello (Eds.), The Origin and Diversification of Language. California Academy of Sciences, San Francisco, California, pp. 1–20.

Marler, P., Slabbekoorn, H., 2004. Nature's music: the science of birdsong. Academic Press.

Martinet, A., 1949. La double articulation linguistigue. Cercle Linguist. Cph. 5, 30–37.

McGregor, W.B., 2009. Linguistics: An Introduction. Continuum, London, UK.

Miller, J.F., Chapman, R.S., 1981. The relation between age and mean length of utterance in morphemes. J. Speech Lang. Hear. Res. 24, 154–161.

Nowak, M.A., 2000. Evolutionary biology of language. Philos. Trans. R. Soc. B Biol. Sci. 355, 1615–1622. doi:10.1098/rstb.2000.0723

Nowak, M.A., Komarova, N.L., 2001. Toward an evolutionary theory of language. Trends Cogn. Sci. 5, 288–295.

Nowak, M.A., Krakauer, D.C., 1999. The evolution of language. Proc. Natl. Acad. Sci. 96, 8028–8033. doi:10.1073/pnas.96.14.8028

Ouattara, K., Lemasson, A., Zuberbühler, K., 2009. Campbell's monkeys use affixation to alter call meaning. PloS One 4, e7808. doi:10.1371/ journal.pone.0007808

Payne, R.S., McVay, S., 1971. Songs of humpback whales. Science 173, 587–597.

Rasa, O.A.E., 1986. Coordinated vigilance in dwarf mongoose family groups: The 'watchman's song' hypothesis and the costs of guarding. Ethology 71, 340–344. doi:10.1111/j.1439-0310.1986.tb00598.x

Rasa, O.A.E., 1977. The Ethology and Sociology of the Dwarf Mongoose (*Helogale undulata rufula*). Z. Für Tierpsychol. 43, 337–406. doi:10.1111/j.1439-0310.1977.tb00487.x

Robinson, J.G., 1984. Syntactic structures in the vocalizations of wedge-capped capuchin monkeys, *Cebus olivaceus*. Behaviour 46–79. doi:10.1163/156853984X00551

Sandler, W., Aronoff, M., Meir, I., Padden, C., 2011. The gradual emergence of phonological form in a new language. Nat. Lang. Linguist. Theory 29, 503–543.

Sandler, W., Aronoff, M., Padden, C., Meir, I., 2014. Language emergence: Al-Sayyid bedouin sign language. Camb. Handb. Linguist. Anthropol.

Senghas, A., Coppola, M., 2001. Children creating language: How Nicaraguan Sign Language acquired a spatial grammar. Psychol. Sci. 12, 323–328. doi:10.1111/1467-9280.00359

Senghas, A., Kita, S., Özyürek, A., 2004. Children creating core properties of language: Evidence from an emerging sign language in Nicaragua. Science 305, 1779–1782. doi:10.1126/science.1100199

Seyfarth, R.M., Cheney, D.L., 2010. Production, usage, and comprehension in animal vocalizations. Brain Lang. 115, 92–100. doi:10.1016/j.bandl.2009.10.003

Sharpe, L.L., Joustra, A.S., Cherry, M.I., 2010. The presence of an avian co-forager reduces vigilance in a cooperative mammal. Biol. Lett. 6, 475–477. doi:10.1098/rsbl.2009.1016

Suzuki, T.N., Wheatcroft, D., Griesser, M., 2016. Experimental evidence for compositional syntax in bird calls. Nat. Commun. 7, 10986. doi:10.1038/ncomms10986

Szathmáry, E., Maynard Smith, J., 1995. The major evolutionary transitions. Nature 374, 227–232.

Tomasello, M., 2003. Constructing a language: A usage-based theory of language acquisition. Harvard University Press.

von Humboldt, W., 1999. On language: on the diversity of human language construction and its influence on the mental development of the human species. Cambridge University Press, Cambridge, UK.

Yip, M.J., 2006. The search for phonology in other species. Trends Cogn. Sci. 10, 442–446.

CHAPTER 1:

Language Evolution: Syntax before Phonology?

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Left: putty-nosed monkey; Top right: Campbell monkey; Bottom right: banded mongooses.

ABSTRACT

Phonology and syntax represent two layers of sound combination central to language's expressive power. Comparative animal studies represent one approach to understand the origins of these combinatorial layers. Traditionally, phonology, where meaningless sounds form words, has been considered a simpler combination than syntax, and thus should be more common in animals. A linguistically informed review of animal call sequences demonstrates that phonology in animal vocal systems is rare, whereas syntax is more widespread. In the light of this and the absence of phonology in some languages, we hypothesize that syntax, present in all languages, evolved before phonology.

Key-Words: *Human language – Animal communication – Evolution – Syntax – Phonology – Comparative approach*

INTRODUCTION

Human language and its origins have intrigued philosophers and scientists since early antiquity [1]. This is unsurprising, as language is responsible for much that distinguishes humans from other species and makes us so successful, including the transmission of knowledge [2–5]. Unfortunately, the search for the origins of language is complicated by the fact that language, unlike other biological traits, does not fossilize or leave any traces to study its cumulative evolution. Empirical studies must therefore circumvent this problem and various different approaches have been undertaken to attempt to unpack the evolution of language [6–8]. These include, among others, the study of child language acquisition [9], hominid morphology [10–12], genetics [13] and the use of computer simulations to test specific hypotheses [14–16].

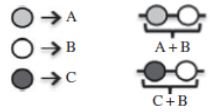
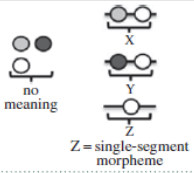
One method that has received particular attention is the exploration of similarities and differences between human language and animal communication systems [6,17]. If similarities are found between humans and a closely related species, then it is possible that they are derived from the same feature present in their common ancestor, representing homologues [18]. If, on the other hand, similarities are found between humans and more distantly related species, these features represent analogues and hence do not give any information on the phylogenetic origins of the feature, but can help elucidate the environmental or social conditions favourable to its convergent evolution [4].

One particular feature of human language that has received considerable attention by both linguists and animal communication researchers, and been highlighted as a ‘fundamental universal structural characteristic’ [19], is duality of patterning [20,21]. Also known as double articulation [22], duality of patterning is a property of language that allows a combinatorial structure on two levels: (i) phonology, where meaningless sounds called phonemes (i.e. the smallest meaning-differentiating elements of a language that do not themselves have meaning) can be combined into morphemes (i.e. the smallest meaningful elements) and words; and (ii) syntax, in which these morphemes and words can be combined into larger structures [23]. Critically, duality of patterning is the property that allows human languages to create a large lexicon from a few distinct signals [21,24–26]. Unpacking the evolutionary route that led to duality of patterning is thus considered central to a more holistic understanding of language evolution.

Researchers of vocal communication in animals have emphasized the fact that animals are also capable of forming different types of sound combinations that could potentially be analogous

or homologous to one or both levels of duality of patterning found in human languages [27–31]. Peter Marler played an important role in establishing the link between the levels of patterning found in human language and the different types of call combinations found in animal communication by introducing the terms phonological and lexical syntax, loosely based on the two levels of duality of patterning [32]. Marler defined phonological syntax (or phonocoding) as the level at which meaningless sounds are combined into sequences, and lexical syntax (or lexicoding) as the higher level at which the meaningful elements are combined. More recently, Hurford has used the terms combinatorial syntax (or combinatoriality) and compositional syntax (or compositionality) to designate the same phenomena as phonological and lexical syntax, respectively [26] (see table 1 for the terms and definitions of sound combinations used in animal communication research and their linguistic equivalents). Our goal here is to examine several examples of animal call combinations from a linguistic perspective and determine which level of duality of patterning they most resemble.

Table 1: Terms and definitions of different types of sound combinations used in animal communication research (non-bold type) and in linguistics (bold). In the visual representation, the circles of different colours on the left represent the different sounds to be combined, they can either have a meaning (represented by a letter as in the case of lexical syntax) or they can have no meaning. On the right, the series of circles represent call combinations that can have a meaning that is function of the meaning of its parts (e.g. A + B), no meaning or a new meaning (e.g. X).

animal communication	human language	definitions	visual representation
lexical syntax lexicoding compositional	grammar (syntax and morphology)	**the way meaningful parts (morphemes, words) go together to form sentences** a sequence of meaningful elements whose meaning is a function of the meaning of the individual elements that compose it and the way they are structured together	
phonological syntax phonocoding combinatorial	idioms (lexicon)	**an expression whose meaning is not predictable from the parts that compose it**	
	phonetics	**the physical properties of sounds (phones)** meaningless sounds are combined into sequences, the sequences obtained having no conventional meaning	
	phonology phonemics	**minimal meaning-differentiating units (phonemes) that do not themselves bear meaning recombine to create meaningful expressions** meaningful elements combine into a meaningful sequence whose meaning is not a function of the meaning of the parts.	

EXAMPLES OF COMBINATIONS IN ANIMAL COMMUNICATION SYSTEMS

Winter Wrens: Phonological Syntax?

Some of the best-studied examples of animal sound combinations come from birdsong [33]. One classic example of phonological syntax noted by Marler is the song of the winter wren (*Troglodytes troglodytes*) [32]. Kroodsma & Momose [34] describe the songs of a Japanese population of winter wrens whose song types consist of a highly predictable sequence of notes or syllable types (a note being a continuous trace on a sonogram and a syllable being a repeated unit of identical notes or groups of notes). In their study population, the typical repertoire for a male includes six or seven song types. These different song types are obtained by reusing many of the same syllables or syllable sequences in a different order. However, as Marler noted, these syllables do not differentiate the song types from one another. In fact, all six or seven song types in a male wren's repertoire convey the same 'message' and none of them have any referential meaning [32]. Therefore, while superficially there seem to be structural similarities between bird song and human phonology, there are important differences when it comes to meaning differentiation. For the wren's song to have phonology in the linguistic sense, the different order of syllables in the different song types would have to bring about a change in meaning between the song types, just as in English *pat* and *tap* differ in meaning but are made up of the same sounds in a different order. Because of this, the structure of the wren's song (and that of most other bird and whale songs) would be better described not as phonological syntax but as phonetic patterning. Phonetics describes the physical properties of sound and, unlike phonology, it does not presuppose that sound patterns carry any function that serves to differentiate meanings.

Despite these critical differences, the search for comparative examples of phonology in animal communication has, in a similar way to Marler, continued to focus on bird [35,36] or whale song [37,38]. However, a more phoneme-focused approach could be taken by searching for the use and comprehension of minimal pairs (pairs of meaningful signs or words distinguished by only one element drawn from a finite list; such as *tap* versus *lap* in English) in animal communication systems [39].

Campbell Monkeys: Lexical Syntax

Both Marler and Hurford argue that lexical syntax is only found in human language [26,32]. However, at least one example of call combination in an animal communication system could correspond to its definition. This is the use of an affixation system by Campbell monkeys (*Cercopithecus campbelli campbelli*) [40]. Campbell monkeys have two main predators: leopards (*Panthera pardus*) and crowned eagles (*Stephanoaetus coronatus*). The Campbell monkeys give a 'krak' call when they detect a leopard and a 'hok' call when they detect a crowned eagle. They can also add an affix '-oo' to both of these calls to produce two new calls: 'krak-oo' and 'hok-oo'. The 'krak-oo' call is given to any general disturbance and the 'hok-oo' call is given to any disturbance in the canopy. The critical aspect here is that the same '-oo' is affixed to both calls ('krak' and 'hok'). It is this use of the same elements, with the same meanings, in different sequences, that makes them compositional rather than combinatorial. The affixation modifies the meaning of the stem calls in a predictable way: changing a call designating a specific predator into a call designating a less specific disturbance in the same general physical space. Perhaps the closest language analogy would be the suffix '-like', changing the meaning of the call from 'leopard' to 'leopard-like (disturbance)'. The meaning of this suffix is fairly abstract: it does not refer to a concrete entity of its own, but directs the hearer to imagine a general situation that is disturbing in a similar way to the presence of a predator yet is not as dangerous as a real appearance of the predator. Abstract meaning operators of this kind are ubiquitous in human languages. Here, Campbell monkeys put together elements that conserve their meaning no matter what sequence they are part of, and obtain assemblies whose meaning reflects the meaning of their parts. This fits Hurford's definition of compositional syntax [26] and so deserves the name syntax, even if it is only a very rudimentary one.

Putty-Nosed Monkeys: A Less Clear-Cut Example

The putty-nosed monkey's (*Cercopithecus nictitans*) combinatorial system is not so easy to categorize. In their communication system described by Arnold & Zuberbühler, putty-nosed monkeys produce two different loud calls: 'pyows' and 'hacks' [41]. These calls can be used as alarm calls when a predator is detected. If the predator is a leopard, the putty-nosed monkeys use 'pyows', and if it is a crowned eagle, they use 'hacks'. In addition to this, the monkeys can combine these two calls into another structure, the 'pyow-hack sequence'. This sequence

normally consists of two to three ‘pyows’ followed by up to four ‘hacks’. The ‘pyow-hack sequences’ elicit the movement of the group. While the components of this sequence bear meaning individually, the meaning of the sequence does not appear to derive from the meaning of these components, and so this combination does not conform to Marler’s definition of lexical syntax [32]. There do, however, exist three alternative analyses that can be invoked to linguistically categorize and understand this call combination in relation to human language.

First, this communication system can be interpreted as a simple phonological system. Under this analysis, the ‘pyows’ and the ‘hacks’ of the putty-nosed monkeys would be considered as phonemes in the linguistic sense, elements carrying no meaning per se but allowing the differentiation between the two single-segment morphemes (i.e. meaningful elements made up of only one sound) ‘pyow’ (‘leopard’) and ‘hack’ (‘eagle’), and a morpheme composed of a sequence, ‘pyow-hack sequence’ (‘let’s go’). Thus, the element ‘pyow’ in the single call ‘pyow’ and in the ‘pyow-hack’ would be comparable to, say, the sound *s* in the single-segment morpheme *s* (as in *John’s*) and in the sequence *so* or *us*—with no meaning in common, but serving as a diacritic for distinguishing meanings.

However, the data also allow alternative analyses that do not assume phonology and duality of patterning. Under one analysis, it would be possible to analyse the ‘pyow-hack sequences’ as idioms, where the original meanings of ‘pyow’ and ‘hack’ have become blurred. A possible etymology is this: the sequence first meant ‘leopard and eagle’ and then, derived from this by implication, ‘danger all over’. This in turn came to mean ‘danger all over, therefore let’s go’ and finally just ‘let’s go’. The human language analogue would be expressions like *kick the bucket*, the meaning of which is no longer transparently related to the meaning of the components, but has undergone complex etymological developments.

Alternatively, under another analysis, one could ascribe much more abstract meanings to ‘pyow’ and ‘hack’, such as ‘move-on-ground’ and ‘move-in-air’. When produced on their own, listeners would seek the contextually most relevant and most suitable interpretation of these calls, possibly using similar heuristic processes such as are well established for human communicators in the theory of implicature inferences [42–44]. A default and common implicature would be, in the case of ‘pyow’, inference to a prototypical danger on the ground, a leopard; and, in the case of ‘hack’, a prototypical danger in the air, an eagle. Since under this analysis the calls themselves have very abstract meanings, it is possible to analyse pyow-hack sequences as lexical compositions: meanings like ‘move-on-ground’ and ‘move-in-air’

combine to a general meaning like ‘we move; let’s go’ since putty-nosed monkeys themselves move both in the tree canopy and, though more rarely, on the ground [45].

Under either of these last two analyses, putty-nosed monkeys would, contrary to Arnold & Zuberbühler’s conclusions [28], have *lexical syntax* in Marler’s sense. At first sight, these alternative analyses are perhaps less plausible than positing phonology because they ascribe more complex cognitive processing to the monkeys: language change in the idiom-based analysis or abstract semantics and a well-tuned pragmatic inference machinery in the compositionality-based analysis. However, the communication system of the Campbell monkeys, a species closely related to the putty-nosed monkeys, suggests that their possible use of lexical syntax with abstract semantics is especially worth considering and should not be ruled out *a priori*.

Banded Mongooses: A Non-Primate Example of Lexical Syntax?

Potential examples of lexical syntax are not limited to primate species: there are also examples from species more distantly related to humans, such as the close calls of the banded mongoose (*Mungos mungo*) [29]. Banded mongooses emit close calls while looking for food and these calls differ in structure depending on the exact nature of the behaviour: digging, searching in the same foraging patch or moving between two patches. In all these contexts, the close call begins with an initial noisy segment that encodes the caller’s identity, which is stable across all three contexts. Additionally, in the searching and moving context, there is a second tonal harmonic segment that does not encode identity; however, its length varies consistently with context, the segment being longer when the mongoose is moving rather than searching. These two segments, noisy and harmonic, come together in the call and indicate both the caller’s identity and his activity.

As with the putty-nosed monkeys, it is possible to interpret these calls as a simple phonological system, with the noisy segment and short and long harmonic segments being three distinct phonemes. The noisy segment can then be produced alone as a single-segment morpheme when digging, or in combination with one of the other ‘phonemes’, which allow distinguishing between the different two-segment morphemes for searching or for moving.

In another interpretation, the banded mongoose close calls can act in an analogous way to short sentences: noisy segment + Ø → ‘I (Fred) dig’; noisy segment + short harmonic segment → ‘I (Fred) search’; noisy segment + long harmonic segment → ‘I (Fred) move’; with the noisy

segment acting as a referential expression that also encodes individual identity (somewhat like the caller's name) and the tonal segment as the 'predicate' that can be compared to simple subject–predicate compositions in human languages. Indeed, some human languages also use individually distinct expressions (i.e. personal names) in lieu of first-person pronouns. This is the case, for example, in Thai, where the use of first-person pronouns equivalent to 'I' is rude. Instead people routinely use their personal name instead of a first-person pronoun, for example saying 'Bill is cooking' while referring to oneself [46]. Under this analysis, the meaning of the assemblies produced by banded mongooses directly reflects the meaning of their different components, making these combinations, in a similar way to the Campbell monkeys', syntactic.

For now, either interpretation is possible, particularly because, in the absence of playback experiments, it is not clear what information listeners extract from these calls. Such experiments are therefore vital in helping shed light on whether banded mongoose close calls represent a syntactic or phonological system.

EXAMPLES FROM HUMAN LANGUAGES WHERE PHONOLOGY IS ABSENT

While in animal communication systems sound combinations seem to be the exception, in human language they are the rule: all human languages combine words at the syntactic level and nearly all human languages, spoken or signed, have phonology, or cherology as it is known for sign languages. However, there do exist some languages possessing features without phonology, or lacking phonology altogether. Understanding why this structural feature of language is and can be absent could shed important light on the origins of syntax and phonology in human languages.

Al-Sayyid Bedouin Sign Language

Most sign languages have phonology (cherology). This was first determined by Stokoe [47] in his work on American Sign Language (ASL). Stokoe specifically demonstrated that ASL has three major categories (hand shape, location and movement) and that they each contain a certain number of features. Replacing one of these features by another causes a change in the meaning of the sign. This allowed Stokoe to conclude that ASL was not made up of holistic signs but of meaningless elements that are recombined into words.

Currently, one sign language is known that does not have phonology, or at least phonology has not fully developed throughout its entire lexicon. This is the Al-Sayyid Bedouin Sign Language (ABSL) described by Sandler et al. [48]. ABSL is a relatively new language used in the Al-Sayyid Bedouin group of the Negev region of Israel. The first deaf members of the group were four siblings born around 75 years ago. Over the next two generations, the number of deaf members increased as more were born into the community, most probably due to recessive congenital deafness [48]. There are now around 120–150 deaf members for a total of around 4000 members. ABSL is also used by a significant proportion of hearing members of the community.

Sandler et al. [48] looked for phonology in ABSL by searching for minimal pairs. For sign language, these can be distinguished by location, orientation, hand shape or movement. The authors did not find minimal pairs in ABSL [48]. On the contrary, they found a great variety in the signs for single words. For example, the sign for 'tea' can be represented by three different hand shapes and the sign for 'dog' can be made either in front of the mouth or in front of the torso (difference in location), depending on the signer. This lack of minimal pairs lead Sandler et al. to conclude that ABSL has no phonology and thus no duality of patterning [48]. Despite its lack of duality of patterning, from a linguistic point of view ABSL is a fully operational language, both in its function, allowing users to have conversations, make plans, tell stories and give instructions, and linguistically, having grammatical regularity at the syntactic, morphological and prosodic levels.

Spoken Languages

Of course, it could be that absence of duality of patterning is a peculiarity of an emerging communication system such as ABSL. However, although the spoken languages studied so far undeniably present duality of patterning, it is not implausible to assume, as does Blevins, that duality of patterning is not an absolutely universal property. Blevins discusses segment-sized morphemes in a number of languages [49]. An example is the English morpheme *s*, which can mean 'plural' (*book*-*s*), 'third-person singular present' (*she look*-*s*) or 'possessor' (*Rik's*). The reason we analyse s as three morphemes with a phoneme /s/ is because the same phoneme recurs in a great number of other morphemes (*soup*, *test*, *miss*, etc.). If this were not the case, one could just as well say that we have a meaning-bearing segment s that happens to be three-ways ambiguous. If a language has a large inventory of such meaning-bearing segments and

the meanings are sufficiently abstract, this would easily allow a sizeable expressive power without duality of patterning. The two critical requirements for this—abstract meanings and large inventories of segments—are both well established in extant languages.

First, there are languages whose lexicon is composed of words with highly abstract meanings. Consider, for example, words like *st'uswalíć ´* 'I picked up the rag' in the North American language Atsugewi, which is composed of a prefix *s'w-* for 'I' followed by the three morphemes *tu* 'do something by hand', *swal* 'for limp (not stiff or resilient) material to move or be located' and *ić* 'upward' [50]. In such a system, a limited number of abstract meanings are strung together and then subjected to a rich machinery of pragmatic inference, deriving concrete meaning effects.

Second, there are languages with impressively large segment inventories. The known maximum is found in !Xõõ in Botswana, with 164 segmental phonemes [51]. Many languages in addition have suprasegmental features like tone (as also found in !Xõõ), vowel and consonant lengthening, nasalization (e.g. *owoku* 'house' versus *õ˜wõŋgu* 'my house' in the Terena language of Brazil [52]) and holistic sound sequences such as are found in interjections (e.g. *ʔm̩ ˈhm̩* for 'yes' and *ʔm̩ ˈʔm̩* for 'no' in English). It is easy to imagine that all these possibilities co-occur in a single language, so that inventories quickly reach between 160 and 180 units, each carrying its own abstract meaning.

Furthermore, Blevins notes that in many languages, meanings depend on position and context [49] (just as the English *-s* means different things depending on whether it follows a noun or a verb stem; cf. above). Even just distinguishing word-initial and word-final positions in two-segment words would thus already yield a potential for more than 300 meanings; adding a noun versus verb distinction could double this number again. Finally, as Blevins also observes, many languages have what are called bi-partite or tri-partite stems, where stems are non-transparently composed of morphemes, like idioms (cf. e.g. in Andi, a language of the Caucasus, *abcho* 'someone washed it', with the bipartite stem *a-ch* 'wash', interrupted by an agreement marker *b-* and followed by a past tense marker *-o* [53]). This quickly adds a few hundred other meanings (in fact, with 180 units that can freely combine with each other in first and second part, a language could potentially have up to 180^2 bipartite stems, which is already beyond an average speaker's lexicon in daily use). Given all these possibilities, it is perfectly possible that there might have been (or will be) a spoken language in the world that lacks duality of patterning. The lexicon of such a language might not (easily) allow growth on the scale of

languages with duality of patterning, but if we also allow for borrowing words from other languages, even these limitations are not as detrimental as one might think.

DISCUSSION

Syntax before Phonology

The examples discussed in this review demonstrate that (i) while phonology in the linguistic sense seems to be rare in animal communication systems, lexical syntax seems to be more widespread than previously thought, and (ii) while there is no human language without syntax, it seems possible for some human languages to lack phonology. This appears to indicate that a single layer of compositional structure (syntax) is less complex to develop than adding to this an extra layer of phonological structure. This leads us to hypothesize that, contrary to the traditional view in both linguistics and animal communication research [54], syntax developed before phonology in human languages.

This hypothesis seems to be further supported by the fact that human languages lacking phonology but possessing syntax, such as ABSL, are emerging languages that do not yet seem to be fully formed. This suggests that syntax develops first to allow the expression of more concepts with only a few words, while phonology appears later on in the development of a language, when the need for a larger vocabulary makes it a more efficient way to produce an increased number of words. If this is the case, we would expect any new emerging languages to present a similar pattern, with syntax developing before phonology. Preliminary surveys suggest that this may be the case for most spontaneous sign languages [55]. In terms of spoken languages, it is harder to search for similar developmental patterns, as emerging spoken languages such as pidgins and creoles are created when people who speak different languages need to communicate. Therefore, these languages are not created from scratch and their sound system is most often taken from one of the original languages [56].

Why syntax developed before phonology is of course open to discussion, but it could be that, from a cognitive perspective, syntax is simpler to process than phonology. Intuitively, it would seem that syntactical combinations would require less memorizing, as only the meanings of the individual signals would need to be learned and remembered, the meaning of the combination being derived from them. For phonological combinations, on the other hand, it would seem that a new meaning has to be learned for each different sequence of sounds.

Insights into the Origins of Syntax and Phonology

While the examples analysed in this review can give some insight into the order of development of different types of sound combinations, they also allow us to formulate hypotheses regarding the conditions favouring their evolution. One obvious similarity between the species demonstrating combinations of meaningful calls is that they all reside in groups characterized by high sociality. This social dimension may well require such species to express more concepts than would be possible with only the individual calls from their anatomically constrained vocal repertoire. One solution to this constraint is to develop a more open-ended vocal repertoire through learning, as is the case in a number of bird species and social mammal species [57]. Alternatively, as we see here, calls could be flexibly combined to express related (compositional syntax) or even unrelated (combinatorial syntax) meanings [41].

Furthermore, of the three major examples we present, two represent call combinations used in less urgent situations. In the case of the Campbell monkeys signallers use single alarm calls on their own to indicate a predator, whereas they use the affixed call for a more general, less immediately threatening disturbance. In a similar way, banded mongoose call combinations occur while foraging rather than in immediate predation contexts. As a shorter time between the perception of the danger by the emitter and the reaction of the receiver would be more advantageous in urgent situations, one might predict clearer evidence for syntax in more relaxed, social contexts [58]. Indeed, for human language, it is well established that more complex and elaborate kinds of syntax are better represented in written than in spoken language [59] (i.e. in a mode of language use that is removed from the rapid and socially challenging interactions that characterize spoken language).

Given the current absence of unambiguous examples of phonology in the linguistic sense in animal communication systems (i.e. there is no clear evidence of patterns of communication that cannot be explained without assuming phonology), variation among human languages may provide additional insight into the origins of this feature. First, the examples of human language features lacking phonology, such as segment-sized morphemes or holistic sound sequences, suggest that duality of patterning is an empirically observed correlation and not a logically necessary property of language [48]. New observations are constantly providing additional empirical data to be interpreted. Second, the absence of phonology in certain aspects of languages, or even in whole languages, points towards a non-genetic basis for this feature in human language. Like songbirds [35] and some mammal species (cetaceans [60], pinnipeds

[61], elephants [62], bats [63]), humans are vocal learners capable of producing a large number of different sounds. However humans are, as far as we know, the only species that use these sounds phonologically to distinguish between the meanings of two sequences. This suggests that vocal learning and the capacity to produce a large number of different sounds alone are not sufficient to induce the emergence of a phonological level. We therefore argue that the constraints leading to the use of a phonological level are more likely to be cognitive in nature rather than linked to the production capacity of a given species. Specifically, once humans developed the cognitive capacities to memorize phonological combinations and their meanings, phonology itself could become subject to cultural, as opposed to biological, evolutionary processes [23,64]. If this is the case, it might explain why phonology in the linguistic sense is so rare in the communication systems of other species.

The constraints driving the cultural evolution of phonology should be widespread across human cultures, reflecting the distribution of the property itself. These constraints could include the need for distinctiveness and learnability, as well as a tendency to keep meaningful distinctions while trying to make an utterance sound similar to other utterances in a population [23]. As Hockett noted, phonology is most efficient when there is a large set of meanings to be expressed, because the combination of phonemes is generally less constrained than the combination of morphemes: the combination of morphemes must 'make sense' [24]. ABSL may lack phonology because it does not currently have these constraints. It is a small community language and its users know each other, potentially making pragmatics and inference an important part of their communicative understanding. However, if the use of ABSL were to spread to a larger population of signers, we could expect a gradual emergence of phonology. In fact, ABSL already seems to have a blueprint for the development of phonology, with the emergence of categories, the regularization of signs within familylects and young signers using conventionalized signs rather than iconic ones [48].

Conclusion

Duality of patterning is considered an important feature of language. From a comparative perspective, this has led to great interest in animal call combinations and their similarities to the two levels of structure found in duality of patterning: phonology and syntax. In this review, we have shown that there exist no clear examples for phonology in the linguistic sense in animal communication systems, and that, contrary to traditional thought, syntax or compositionality is

actually more widespread. When also analysing the structure of human languages, we found that some parts of some languages, and at least one entire language, do not display phonology. From these observations, we alternatively argue that syntax developed before phonology and that the former seems to be a cognitively simpler process, with the latter possibly being the product of cultural evolution. This could be taken into account in future research on meaningful animal call combinations by assuming lexical, and not phonological, syntax as the simplest explanation.

If a certain language property, such as phonology, is not universally present in all human languages, then it is probably unsurprising that it is non-existent in a large number of animal communication systems. However, if the factors leading to the presence (or absence) of this property can be determined, they may allow us to make predictions on which species or social contexts to focus our research effort to find these analogous or homologous properties in animal communication systems if they do exist. This focus fits with recent developments in linguistics that increasingly challenge the idea of a given set of properties defining all and only human languages, and instead probe into the social and biological factors that condition how specific properties of language arise, develop and disappear again in the course of time [65–67].

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REFERENCES

1. Aristotle 350 BC. The history of animals. (Reprinted by Kessinger Publishing 2004.)
2. Darwin C. 1871 The descent of man and selection in relation to sex. New York, NY: D. Appleton and Company.
3. Tomasello M. 2008 Origins of human communication. Cambridge, MA: MIT Press.
4. Fitch WT, Huber L, Bugnyar T. 2010 Social cognition and the evolution of language: constructing cognitive phylogenies. Neuron 65, 795–814. (doi:10.1016/j.neuron.2010.03.011)
5. Hurford JR. 2007 The origins of meaning: language in the light of evolution. Oxford, UK: Oxford University Press.
6. Hauser MD, Chomsky N, Fitch WT. 2002 The faculty of language: what is it, who has it, and how did it evolve? Science 298, 1569–1579. (doi:10.1126/ science.298.5598.1569)
7. Christiansen MH, Kirby S. 2003 Language evolution: consensus and controversies. Trends Cogn. Sci.
8. Gong T, Shuai L, Wu Y. 2013 Multidisciplinary approaches in evolutionary linguistics. Lang. Sci. 37, 1–13. (doi:10.1016/j. langsci.2012.09.002)
9. Tomasello M. 2003 Constructing a language: a usage-based theory of language acquisition. Cambridge, MA: Harvard University Press.
10. Lieberman P. 1973 On the evolution of speech. In Festschrift for Morris Halle (eds S Anderson, P Kiparsky), pp. 107–127. New York, NY: Holt, Rinehart and Winston.
11. Lieberman P. 1984 The biology and evolution of language. Cambridge, MA: Harvard University Press.
12. Lieberman P. 1998 Eve spoke: human language and human evolution. New York, NY: W. W. Norton.
13. Enard W, Przeworski M, Fischer SE, Lai CS, Wiebe V, Kitano T, Monaco AP, Pääbo S. 2002 Molecular evolution of FOXP2, a gene involved in speech and language. Nature 418, 869–872. (doi:10.1038/ nature01025)
14. Deacon TW. 2003 Universal grammar and semiotic constraints. In Language evolution (eds MH Christiansen, S Kirby), pp. 111–139. Oxford, UK: Oxford University Press.
15. Kirby S. 2001 Spontaneous evolution of linguistic structure: an iterated learning model of the emergence of regularity and irregularity. IEEE J. Evol. Comput. 5, 102–110. (doi:10.1109/4235.918430)
16. Nowak MA, Komarova NL. 2001 Toward an evolutionary theory of language. Trends Cogn. Sci. 5, 288–295. (doi:10.1016/S1364-6613(00)01683-1)

17. Zuberbühler K. 2005 The phylogenetic roots of language: evidence from primate communication and cognition. Curr. Dir. Psychol. Sci. 14, 126–130. (doi:10.1111/j.0963-7214.2005.00357.x)
18. Fedurek P, Slocombe KE. 2011 Primate vocal communication: a useful tool for understanding human speech and language evolution? Hum. Biol. 83, 153–173. (doi:10.3378/027.083.0202)
19. Hurford JR. 2002 The roles of expression and representation in language evolution. In The transition to language (ed. A Wray), pp. 311–334. Oxford, UK: Oxford University Press.
20. Hockett CF. 1960 Logical considerations in the study of animal communication. In Animal sounds and communication (eds WE Lanyon, WN Tavolga), pp. 392–430. Washington, DC: American Institute of Biological Sciences.
21. Hurford J. 2008 The evolution of human communication and language. In Sociobiology of communication: an interdisciplinary perspective (eds P D'Ettorre, DP Hughes), pp. 249–264. Oxford, UK: Oxford University Press.
22. Martinet A. 1949 La double articulation linguistigue. Cercle Linguistique de Copenhague 5, 30–37. (doi:10.1080/01050206.1949.10416289)
23. De Boer B, Sandler W, Kirby S. 2012 New perspectives on duality of patterning: introduction to the special issue. Lang. Cogn. 4, 251–259. (doi:10.1515/langcog-2012-0014)
24. Hockett CF. 1960 The origin of speech. Sci. Am. 203, 88–111. (doi:10.1038/scientificamerican0960-88)
25. von Humbolt W. 1836 Uber die Kawi-Sprache auf der Insel Java. Berlin, Germany: Druck-erei der Koniglichen Akademie der Wissenschaften.
26. Hurford JR. 2011 The origins of grammar: language in the light of evolution II. Oxford, UK: Oxford University Press.
27. Zuberbühler K. 2002 A syntactic rule in forest monkey communication. Anim. Behav. 63, 293–299. (doi:10.1006/anbe.2001.1914)
28. Arnold K, Zuberbühler K. 2012 Call combinations in monkeys: compositional or idiomatic expressions? Brain Lang. 120, 303–309. (doi:10.1016/j.bandl. 2011.10.001)
29. Jansen DA, Cant MA, Manser MB. 2012 Segmental concatenation of individual signatures and context cues in banded mongoose (*Mungos mungo*) close calls. BMC Biol. 10, 97. (doi:10.1186/1741-7007-10-97)
30. Hailman JP, Ficken MS, Ficken RW. 1985 The 'chicka-dee' calls of *Parus atricapillus*: a recombinant system of animal communication compared with written English. Semiotica 56, 191–224. (doi:10.1515/semi.1985.56.3-4.191)
31. Freeberg TM, Lucas JR. 2002 Receivers respond differently to chick-a-dee calls varying in note composition in Carolina chickadees, *Poecile carolinensis*. Anim. Behav. 63, 837–845. (doi:10.1006/anbe.2001.1981)

32. Marler P. 1998 Animal communication and human language. In The origin and diversification of language (eds NG Jablonski, Aiello), pp. 1–20. San Francisco, CA: California Academy of Sciences.
33. Berwick RC, Okanoya K, Beckers GJL, Bolhuis JJ. 2011 Songs to syntax: the linguistics of birdsong. Trends Cogn. Sci. 15, 113–121. (doi:10.1016/j.tics.2011.01.002)
34. Kroodsma DE, Momose H. 1991 Songs of the Japanese population of the winter wren (*Troglodytes troglodytes*). Condor 93, 424–432. (doi:10.2307/1368959)
35. Catchpole CK, Slater PJB. 2008 Bird song: biological themes and variations, 2nd edn. Cambridge, UK: Cambridge University Press.
36. Gentner TQ, Fenn KM, Margoliash D, Nusbaum HC. 2006 Recursive syntactic pattern learning by songbirds. Nature 440, 1204–1207. (doi:10.1038/nature04675)
37. Payne RS, McVay S. 1971 Songs of humpback whales. Science 173, 587–597. (doi:10.1126/science.173.3997.585)
38. Suzuki R, Buck JR, Tyack PL. 2006 Informational entropy of humpback whale songs. J. Acoust. Soc. Am. 119, 1849–1866. (doi:10.1121/1.2161827)
39. Yip MJ. 2006 The search for phonology in other species. Trends Cogn. Sci. 10, 442–446. (doi:10.1016/j.tics.2006.08.001)
40. Ouattara K, Lemasson A, Zuberbühler K. 2009 Campbell's monkeys use affixation to alter call meaning. PLoS ONE 4, e7808. (doi:10.1371/journal.pone.0007808)
41. Arnold K, Zuberbühler K. 2006 Language evolution: semantic combinations in primate calls. Nature 441, 303–303. (doi:10.1038/441303a)
42. Grice HP. 1975 Logic and conversation. In Syntax and semantics III: Speech acts. (eds P Cole, JL Morgan), pp.41–58. New York, NY: Academic Press.
43. Sperber D, Wilson D. 1986 Relevance: communication and cognition. Oxford, UK: Blackwell.
44. Levinson SC. 2000 Presumptive meanings: the theory of generalized conversational implicature. Cambridge, MA: MIT Press.
45. Bitty EA, McGraw WS. 2007 Locomotion and habitat use of Stampflii's putty-nosed monkey (*Cercopithecus nictitans stampflii*) in the Taï National Park, Ivory Coast. Am. J. Phys. Anthropol. 134, 383–391. (doi:10.1002/ajpa.20679)
46. Iwasaki S, Horie IP. 2005 A reference grammar of Thai. Cambridge, UK: Cambridge University Press.
47. Stokoe WC. 1960 Sign language structure. Studies in Linguistics, occasional paper 8. Buffalo, NY: Department of Anthropology and Linguistics, University of Buffalo.
48. Sandler W, Aronoff M, Meir I, Padden C. 2011 The gradual emergence of phonological form in a new language. Nat. Lang. Linguist. Theory 29, 503–543. (doi:10.1007/s11049-011-9128-2)

49. Blevins J. 2012 Duality of patterning: absolute universal or statistical tendency? Lang. Cogn. 4, 275–296. (doi:10.1515/langcog-2012-0016)
50. Talmy L. 1972 Semantic structures in English and Atsugewi. Linguistics Department, University of California, CA, USA.
51. Traill A. 1985 Phonetic and phonological studies of !Xäoo Bushman. Hamburg, Germany: H. Buske.
52. Akinlabi A. 1996 Featural affixation. J. Ling. 32, 239–289. (doi:10.1017/S0022226700015899)
53. Bickel B, Nichols J. 2007 Inflectional morphology. Lang. Typol. Syntact. Des. 3, 169–240. (doi:10.1017/CBO9780511618437.003)
54. Fitch WT. 2010 The evolution of language, 1st edn. Cambridge, UK: Cambridge University Press.
55. Meir I, Sandler W, Padden C, Aronoff M. 2010 Emerging sign languages. In Oxford handbook of deaf studies, language, and education. Oxford, UK: Oxford University Press.
56. McGregor WB. 2009 Linguistics: an introduction. London, UK: Continuum.
57. Slater PJB, Janik VM. 2010 Vocal Learning. In Encyclopedia of animal behavior (eds MD Breed, J Moore), pp. 551–557. Oxford, UK: Academic Press.
58. Candiotti A, Zuberbühler K, Lemasson A. 2012 Context-related call combinations in female Diana monkeys. Anim. Cogn. 15, 327–339. (doi:10.1007/ s10071-011-0456-8)
59. Karlsson F. 2010 Syntactic recursion and iteration. In Recursion and human language (ed. H. van der Hulst), pp. 43–67. Berlin, Germany: De Gruyter Mouton.
60. Tyack PL, Sayigh LS. 1997 Vocal learning in cetaceans. In Social influences on vocal development, pp. 208– 233. Cambridge, UK: Cambridge University Press.
61. Schusterman RJ. 2008 Vocal learning in mammals with special emphasis on pinnipeds. In The evolution of communicative flexibility: complexity, creativity, and adaptability in human and animal communication (eds DK Oller, U Gribel), pp. 41–70. Cambridge, MA: MIT Press.
62. Poole JH, Tyack PL, Stoeger-Horwath AS, Watwood S. 2005 Animal behaviour: elephants are capable of vocal learning. Nature 434, 455–456. (doi:10.1038/434455a)
63. Boughman JW. 1998 Vocal learning by greater spear-nosed bats. Proc. R. Soc. Lond. B 265, 227–233. (doi:10.1098/rspb.1998.0286)
64. Tomasello M. 2003 Origins of human communication. Cambridge, MA: MIT Press.
65. Bickel B. 2007 Typology in the 21st century: major current developments. Linguist. Typol. 11, 239–251. (doi:10.1515/LINGTY. 2007.018)
66. Bickel B. In press. Linguistic diversity and universals. In Cambridge handbook of linguistic anthropology (eds N Enfield, J Sidnell, P Kockelman). Cambridge, UK: Cambridge University Press.

67. Evans N, Levinson SC. 2009 The myth of language universals: language diversity and its importance for cognitive science. Behav. Brain Sci. 32, 429. (doi:10.1017/S0140525X0999094X)

CHAPTER 2:

Call Concatenation in Wild Meerkats

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Adult meerkat babysitting pups near the sleeping burrow.

ABSTRACT

Repertoire size, frequently determined by the number of discrete call types, has been used as a means to assess vocal complexity in animals. However, species can also increase their communicative complexity by using graded signals or by combining individual calls together. Animal call sequences can be divided into two main categories, each subdivided into two classes: repetitions, with either an unlimited or finite number of iterations of the same call type, and mixed call combinations, composed of two or more graded or discrete call types. Social contexts involve a wide range of behaviours and, unlike predation contexts, can be associated with both positive and negative emotions. Therefore, interactions linked to social contexts may place additional demands on an animal's communicative system and lead to the use of call combinations. We systematically documented call combinations produced by wild meerkats (*Suricata suricatta*), a highly social carnivore, in social contexts in their natural habitat. We observed twelve distinct call combinations belonging to all four different classes of combination, emitted in all of the observed behavioural contexts. Four combinations were produced in a single context whereas the remaining eight were produced in several contexts, albeit in different proportions. The broad use of combinations suggests that they represent a non-negligible part of meerkat social communication and that they can be used in flexible ways across various behavioural contexts. Comparison with combinations produced in predation contexts indicated that social call combinations are more varied in number of classes and structural complexity than the former, perhaps due to the greater variety of social contexts. However, in meerkats, combinations of functionally referential calls have been documented in predation but not social contexts, suggesting that both social and predation pressures may play a role in the evolution of combinatoriality in animal communication.

Key Words: *Call combination – Social context – Vocal communication – Natural observations - Meerkat*

INTRODUCTION

Communicative complexity related to signal diversity can be measured in two main ways: through assessing the number of distinct signals produced or by calculating the bits of information contained in the system (Freeberg, Dunbar, & Ord, 2012). To date, acoustic communicative complexity has mostly been assessed using vocal repertoire size (Oller & Griebel, 2008). However, most vocal repertoires only list the acoustically discrete call types the species produce and, for the majority of species, the number of these call types is physically constrained, limiting the size of their repertoire (Fitch, 2000). To achieve a higher communicative output despite this limitation, some animal species produce intermediate call types, leading to a graded call system (Marler, 1976). An additional way to increase communicative output is to combine individual calls (Arnold & Zuberbühler, 2006; Engesser, Crane, Savage, Russell, & Townsend, 2015). Combining calls has frequently been argued to be a more efficient way of conveying new messages than creating new calls (Jackendoff, 1999; Nowak, Plotkin, & Jansen, 2000) and may reduce the risk of perception errors from the receiver's side (Nowak & Krakauer, 1999; Nowak, Krakauer, & Dress, 1999).

Through dividing call combinations described in the literature into categories based on the number of component call types, we can identify two main groups: repetitions and mixed call combinations. Repetitions are combinations composed of only one call type and can be subdivided into two classes: unlimited and finite. Unlimited repetitions are combinations that are not characterised by the number of times the call is repeated. Examples of such combinations are corncrakes' (*Crex crex*) aggression calls (Ręk, 2013), and alarm calls emitted repeatedly in many species (non-primate mammals: Blumstein & Armitage, 1997; Manser, 2001; non-human primates: Macedonia, 1990; Lemasson, Ouattara, Bouchet, & Zuberbühler, 2010; Schel, Candiotti, & Zuberbühler, 2010). On the contrary, finite repetitions are always composed of the same number of calls, for example the Bulwer's petrel's (*Bulweria bulwerii*) double calls are always composed of two calls (James & Robertson, 1985).

Here we define mixed call combinations as sequences that include at least two different call types and can be either graded or discrete or both. Graded call combinations are sequences of calls that grade along a structural or temporal continuum between two discrete call types (Keenan, Lemasson, & Zuberbühler, 2013). Gradation can occur in the frequency parameters (e.g. peak frequency, frequency range), amplitude, or duration of the call. Examples of such combinations can be found in diverse taxa from amphibians to non-human primates (hereafter

primates). One case of such a graded sequence is the Blanchard's cricket frog's (*Acris crepitans blanchardi*) aggression calls that become more aggressive with the approach of a simulated intruder (Wagner Jr, 1989), as expressed in the calls by an increase in length and number of pulses. In another case, the Senegal bushbaby (*Galago senegalensis senegalensis*) produces sequences of calls when excited that grade from one call type to another as the caller gets more aroused (Zimmermann, 1985). Moreover, combinations may contain graded calls that are not graded into each other during the sequence, as seen in banded mongoose (*Mungos mungo*) lost sequences that contain both close calls and lost calls, which are two distinct graded calls (Jansen, 2013). Discrete mixed call combinations are composed of several discrete call types with no intermediate forms. For example, male Túngara frogs (*Physalaemus pustulosus*) produce calls composed of two distinct components, a whine followed by up to six chucks to attract females (Ryan, 1980). In primates, female Diana monkeys (*Cercopithecus diana*) produce several social calls, used to communicate over short distances with other group members in non-predatory contexts, in combinations integrating two distinct call types (Candiotti, Zuberbühler, & Lemasson, 2012). Examples of discrete mixed call combinations include the assembly of functionally referential acoustic units resulting in a new or related meaning, as seen in the alarm call systems of some forest guenon species (putty-nosed monkeys, *Cercopithecus nictitans*: Arnold & Zuberbühler, 2006; Campbell monkeys, *Cercopithecus campbelli*: Ouattara, Lemasson, & Zuberbühler, 2009).

Recent attention has focused on call combination production in non vocal-learning species. Unlike vocal learning species such as songbirds, hummingbirds, and parrots in birds, and humans, some marine mammals, and bats in mammals (Slater & Janik, 2010), non vocal-learners cannot expand their vocal repertoire by learning to produce new sounds. Hence non vocal-learning species could be expected to use call combinations as a means to increase their communicative output (Nowak & Krakauer, 1999; Nowak et al., 1999). Many studies on call combinations in animal communication systems have focused on non-human primates, in particular their alarm or long calls (black-fronted titi monkeys, *Callicebus nigrifrons*: Cäsar, Byrne, Young, & Zuberbühler, 2012; Bornean orang-utans, *Pongo pygmaeus wurmbii*: Spillmann et al., 2010; Campbell monkeys: Ouattara et al., 2009; putty-nosed monkeys: Arnold & Zuberbühler, 2006; white-handed gibbons, *Hylobates lar*: Clarke, Reichard, & Zuberbühler, 2006). However, an emerging body of data suggests quieter social calls may represent a suite of calls also open to combinatorial operations (chimpanzees, *Pan troglodytes*: Crockford & Boesch, 2005; bonobos, *Pan paniscus*: Clay & Zuberbühler, 2009; red-capped mangabeys,

Cercocebus torquatus: Bouchet, Pellier, Blois-Heulin, & Lemasson, 2010; Diana monkeys: Candiotti et al., 2012).

It has been hypothesized that, unlike most predation contexts where an immediate change in behaviour in response to a call is adaptive, in the majority of social situations, latency to respond is not necessarily crucial for survival. Therefore both the caller and the receiver should have more time to produce and process longer strings of acoustic units in social contexts (Collier, Bickel, van Schaik, Manser, & Townsend, 2014). Moreover, social contexts can involve a highly variable range of behaviours and, unlike predation contexts, they can be associated with both positive and negative emotions. Thus, interactions during social contexts may place additional demands on the communication system that could promote combinatoriality. Data from primates seem to support this (Bouchet et al., 2010; Candiotti et al., 2012; Clay & Zuberbühler, 2009; Crockford & Boesch, 2005), and some non-primate species have also been described as producing call combinations in non-predation contexts (banded mongooses: Jansen, Cant, & Manser, 2012; corncrakes: Rek, 2013; chestnut-crowned babblers, *Pomatostomus ruficeps*: Engesser et al., 2015). However, a systematic documentation of the presence and extent of combinatorial communication within a species repertoire is rarely undertaken (but see Crockford & Boesch, 2005 for a study on wild chimpanzees and Bouchet et al., 2010 for a study on captive red-capped mangabeys). Quantifying the extent and use of combinations within a species' communication system is key to understanding both the diversity of combinations produced in animal communication, and the extent to which they result from different combinatorial production mechanisms. Furthermore, elucidating the variance in distribution of combination types between social and predation contexts in different species could shed light on interspecies differences and subsequently on the contexts promoting communicative complexity. This could ultimately lead to a better understanding of the factors influencing the evolution of combinatoriality more generally.

Some animal calls have been termed functionally referential due to their high context specificity and link to an external object or event (Macedonia & Evans, 1993), while other calls seem to mainly reflect the animal's internal state and are referred to as motivational/emotional calls (Darwin, 1872; Morton, 1977). An animal's internal state includes both motivation, which is the behavioural state the animal experiences adjusted to its external environment and internal physiological state, and emotion, a short but intense affective reaction to a stimulus which can be measured along two dimensions: arousal (high or low) and valence (positive or negative) (Briefer, 2012). It is now recognised that the same call can encode both types of information,

functional reference and internal state (Manser, Seyfarth, & Cheney, 2002). Given that call combinations are built from several different calls, the combinations themselves have the potential to carry similar types of information, pertaining to the internal state or external event experienced by the signaller. Furthermore, as they comprise several calls, combinations could also inform receivers on mixed motivations/emotions, more than one external event, or even combine the two types of information expressing both the caller's internal state and an external event.

Here, we aimed to test the hypothesis that social contexts promote the production of call combinations in animal communication through investigating the combinatorial vocal behaviour of meerkats. In line with previous work in primates showing broad usage of call combinations in social situations, we expected call combinations to be widely used in social situations. Furthermore, if social contexts represent an additional relevant pressure favourable to the production of call combinations, we would expect meerkats to produce at least the same combinatorial structures with the same relative frequency, in social as in predation contexts.

Meerkats (*Suricata suricatta*) are a highly social species of cooperative breeding mongoose, living in groups of 3 to 50 individuals (Clutton-Brock et al., 2006), with a well-studied vocal repertoire, making them an ideal species in which to explore the extent of call combination production and usage. They possess a rich vocal repertoire consisting of more than 30 discrete and graded call types (see supplementary material; Manser, 1998; Manser et al., 2014). Meerkat call combinations have already been documented in predation contexts (Manser, 2001; Manser, 2009). They produce unlimited repetitions of the same alarm call type such as barks (Manser et al., 2014; Townsend, Charlton, & Manser, 2014). Meerkats also produce graded mixed call combinations in which the aerial or terrestrial alarm calls grade in urgency (Manser, Bell, & Fletcher, 2001). Finally, they emit discrete mixed call combinations consisting of terrestrial predator alarm calls and moving animal alarm calls (Manser, 2009; Manser et al., 2014). However, little is known about meerkats' social call combinations. We therefore established a repertoire of meerkat call combinations produced specifically in social contexts. We analysed in which behavioural contexts call combination types were produced and how context specific they were. Furthermore, to assess if there were systematic differences in composition of the structurally more variable call combinations between contexts, we noted what type the first call was, the proportions of their different component call types and their context specificity.

MATERIAL & METHODS

Study Site and Animals

Long term observational data from the Kalahari Meerkat Project (KMP) collected between 1995 and 2014 has been the basis for identifying the different types of vocal combinations in meerkats. An observer (K.C.) collected systematic data for this study between December 2013 and February 2014. The KMP is located in the South African Kalahari near Van Zylsrus (26°58'S, 21°49'E) (for more details about the habitat and climate of the study site see Clutton-Brock et al., 1998). All meerkats were habituated to human observers to the extent that they allowed detailed observations and recordings within 0.5-3m. All individuals were tagged with subcutaneous transponders as part of the long term data collection of the KMP and marked with a unique combination of dye-marks for identification in the field (Jordan, Cherry, & Manser, 2007).

Recordings and Combination Analysis

We systematically recorded the vocal combinations produced by 47 adult meerkats over one year of age (17 females, 30 males) residing in eight different groups. Ten minute focal recordings (Altmann, 1974) were made using a portable recorder (Roland R-26, Roland Corporation, Hamamatsu, Japan) attached to a directional microphone (Sennheiser ME66/K6, Sennheiser Electronic Corp., Old Lyme, CT, U.S.A.; sampling frequency 44.1 kHz, 16 bits). Comments on the meerkats' behaviour were recorded simultaneously onto the second channel. The focal recordings took place in the morning, between the times when meerkats emerged from the sleeping burrow and when they started to rest during the hottest part of the day and again in the afternoon, from when they resumed foraging until they went back into their sleeping burrow in the evening. These were the periods of the day when the meerkats were the most active, socially and vocally. On average 60 minutes of usable recordings were obtained each day (range: 10 – 130min). The subject's behaviour was classed as belonging to one of eight categories which include the majority of behaviours meerkats perform on a daily basis: relaxed, sunning, babysitting, digging, moving, vigilance, aggression or submission (for definitions see table 1).

In an attempt to document all meerkats' social call combinations, we included 'food aggression call sequences' in our descriptions of meerkat call combinations, despite not recording any during the two month focal observation period. This absence of food aggression call sequences

was potentially due to the high rainfall, and therefore high food availability, during this short study period. Descriptions of this combination were based on spectrograms from our long term recording database. In particular, we used food aggression sequences elicited through food presentation experiments where a focal meerkat was fed a scorpion and its vocalisations were recorded from a close distance. These calls were, however, only used in a descriptive way and were not included in the quantitative analysis.

Praat software (www.praat.org) was used to visualise and categorise the call combinations recorded. Systematically and objectively defining call combinations in animal communication is problematic and many previous studies lack a quantitative approach (Kershenbaum et al., 2014). In line with Crockford and Boesch (2005), who documented the repertoire of social call combinations in chimpanzees, we defined a call combination as a series of two or more calls that was clearly separated from the preceding and following calls by a longer silence than those separating the calls within the combination. These combinations could easily be distinguished by ear and the time separating two calls within a combination was never longer than 1sec and often, depending on the length of the discrete call types comprising the combination, much shorter, in the order of 0.01sec. Based on a randomly selected subset of recordings (amounting to 4.5 hours of recording), mean (±SE) silence duration between two calls within a combination was 0.05±0.003sec (min=0, max=0.36), whereas the mean duration of a silence between two individual calls was 9.6±0.6sec (min=0.03, max=328). Contrary to Crockford and Boesch (2005), however, we also included sequences of the same call type as call combinations as we aimed to document all combinations, including repetitions. The combinations and their individual component calls were identified by visual and audio inspection of the corresponding spectrograms. Additionally, two naïve observers independently classified a randomly selected subset of the call combinations (N=560 combinations, 10% of total dataset). Observer reliability was calculated using Cohen's Kappa coefficients, which indicated substantial agreement (κ=0.74 and κ=0.80) (Landis & Koch, 1977). Combinations were then classified and the context of emission was determined by the behaviour of the caller at that time. To control for a potentially varying number of combinations emitted in each context, we then looked at the proportions of each combination for each behavioural context. For combinations of three or more calls comprising at least two call types, named 'long sequences', the length of the combination in number of calls and the proportions of the different call types in each combination were noted. Given that the first call-type of a sequence may encode initial information or function to alert the receiver, as seems to be the case in certain guenon species

where the first call of a sequence functions as an attention getter (putty-nosed monkey: Arnold & Zuberbühler, 2012), we also specifically noted the first call of the sequence.

Table 1: Description of the behavioural contexts in which the meerkats produced call combinations.

Context	Description
Relaxed	Includes huddling, where several meerkats gather together in a tight group; autogrooming and allogrooming (delBarco-Trillo et al., 2016); contact lying (Habicher, 2009)
Sunning (or sunbathing)	Sitting or standing on hind legs in the sun, often in close proximity to the sleeping burrow (Habicher, 2009)
Babysitting	Remaining at the sleeping burrow with pups while the rest of the group forages (Clutton-Brock et al., 1998)
Digging	Includes foraging for food (Doolan & Macdonald, 1996) and renovating sleeping burrows (Manser & Bell, 2004)
Moving	Walking or running (Habicher, 2009)
Vigilance	Includes sentinel behaviour and scanning the environment for predators while on all fours, sitting or standing on hind legs (delBarco-Trillo et al., 2016)
Aggression	Food competition, displacement and fights (delBarco-Trillo et al., 2016)
Submission	Approaching a dominant individual in a crouched position (delBarco-Trillo et al., 2016)

Statistical Analysis

All statistical analyses were carried out using R version 3.2.1 (R Core Team, 2015) and the package lme4 (Bates, Maechler, Bolker & Walker, 2015) and asbio (Aho, 2016). We compared meerkat production rate of call combinations in different continuous behavioural contexts (babysitting, digging, sentinel and sunning) using a Mack-Skillings test. The Mack-Skillings test is a Friedman-type statistic that can be used for block designs with missing data (Chatfield & Mander, 2009). When a significant result was found, we carried out pairwise Wilcoxon tests and corrected *P*-values for multiple testing using false discovery rate (Benjamini & Hochberg, 1995).

In order to determine if the proportions of each combination type varied in relation to behavioural context we ran a Generalized Linear Mixed Model (GLMM; Baayen, 2008) with a binomial family and a logit link function for each combination type produced in more than one context (8 GLMMs, data obtained from 45 individuals belonging to 8 groups). Context was fitted as fixed effect with random slopes (Schielzeth & Forstmeier, 2009) and individual nested within group as random effect to control for potential group or individual differences. A GLMM of the same format was run for each call type produced in a long sequence (5 GLMMs, N individuals=28, N groups=7) to analyse the proportions of the different call types within the long sequences, again depending on context. Random intercept GLMMs were run for each call type initiating long sequences (4 GLMMs, N individuals=28, N groups=7), to determine if call type initiating long sequences varied with context.

A GLMM (N individuals=28, N groups=7) with a Poisson family and a log link function was used to analyse the number of calls in the long sequence. Context was fitted as fixed effect with random slopes and individual nested within group as random effect. We controlled for over-dispersion of the data by creating an observation level random term that was fitted as random effect (Harrison, 2014).

For all models overall p-values were obtained using likelihood ratio tests, in which the full model was compared to a null model containing only the random factors, slopes and intercept. For pairwise comparisons of contexts, p-values were obtained from the coefficients of the model summary. GLMMs were relevelled to obtain p-values for all pairwise comparisons. When multiple GLMMs were carried out on the same dataset, p-values were adjusted to correct for multiple testing using false discovery rate (Benjamini & Hochberg, 1995).

In order to check whether any one individual strongly affected our results, we re-ran each model, removing sequentially each individual from the dataset, and compared the coefficients to those obtained from the model with the full dataset (Hedwig, Mundry, Robbins, & Boesch, 2014). Where our findings were significant, we observed little variation in the coefficients of the models when an individual was removed from the model. However, there were some appreciable differences in coefficients related to some of our non-significant results, indicating that effects could be stronger than suggested by our models (Hedwig et al., 2014).

Ethical Note

All data collection adhered to ASAB guidelines. This study was purely observational, with no invasive or experimental procedures conducted as part of it. The study population was habituated to observers following them at a close distance all day and to microphones. Care was taken not to disturb the meerkats' daily routine during observations. All research was conducted under the permission of the ethical committee of Pretoria University and the Northern Cape Conservation Service, South Africa (Permit number: EC011-10).

RESULTS

Over a period of two months we obtained more than 2700 minutes (around forty five hours) of focal recordings (mean±SE=57±4 (range 10 to 117) minutes of observation per meerkat). Forty-five out of the forty-seven meerkats produced call combinations (122±20 (range 2 to 571) combinations recorded per meerkat). On average the meerkats that combined calls emitted 2.6±0.7 (range 0.1 to 10.2) combinations per minute of recording. Rate of production of call combinations varied between the different continuous behavioural contexts that typically last more than a few seconds (Mack-Skillings, df=46, MS test statistic=87, $p<0.001$). Subjects produced call combinations at lower rates while digging (0.2±0.1 combinations/min) than while sunning (3.6±0.8 combinations/min), babysitting (5.0±1.4 combinations/min.) or while on sentinel (7.0±1.2 combinations/min) (pairwise Wilcoxon test, respectively $p<0.001$, $p<0.001$ and $p<0.001$).). They also produced combinations at significantly lower rates while sunning than while on sentinel (Wilcoxon test, $p=0.04$). There were no significant differences in combination production rates between sunning and babysitting, and between babysitting and sentinel behaviour (Wilcoxon test, respectively $p=0.33$ and $p=0.34$).

Meerkat Call Combination Types and Contexts of Production

Based on our long-term adlib vocal data and focal recordings over the two-month study period, meerkats produced twelve different types of combinations from seven discrete call types (see figure 1). All four classes, belonging to both categories of combination were represented: unlimited and finite repetitions and graded and discrete mixed call combinations (see table 2). The call combinations differed in how frequently they were recorded during the two-month focal observation period, with 'two short calls' (hereafter sc.2) being recorded the most often (3361 times) whereas 'chatter call sequences' were recorded the least (9 times), and no food aggression call sequences were recorded during the same period (see supplementary material). The discrete call types that were recorded as part of a call combination are described in table 3.

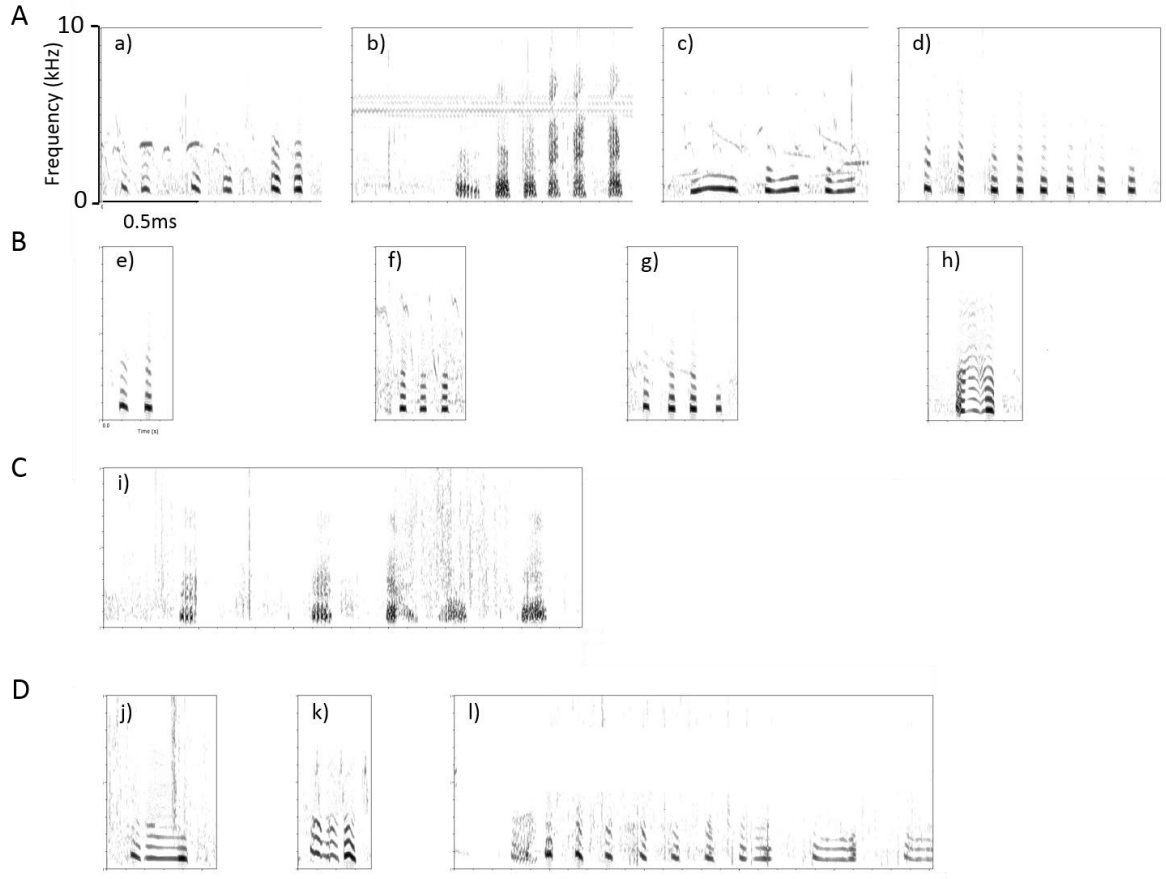


Figure 1: Spectrograms of the different call combinations produced by meerkats. A: unlimited repetitions, including a) submission call sequence, b) chatter call sequence, c) moving call sequence, and d) short call sequence. B: finite repetitions, including e) two short calls, f) three short calls, g) four short calls, and h) quasi-combination. C: graded call combinations, including i) food aggression call sequence. D: discrete mixed call combinations, including j) di-drrr, k) mixed short call sequence and l) long sequence. The time and frequency scales apply to all spectrograms.

Focal subjects produced call combinations in all eight of the predefined contexts: aggression, babysitting, digging, moving, relaxed, submission, sunning and vigilance (see table 1). Four call combinations, composed of context-specific calls, were produced exclusively in one behavioural context. 'Moving call sequences' were only emitted in the moving context, chatter call sequences were emitted only in the aggression context and 'submission call sequences' only in the submission context. Additionally, food aggression call sequences were only obtained during food competition events.

Table 2: The different types of combinations produced by meerkats in non-urgent contexts.

Category	Class	Combination	Description
Repetitions	Unlimited	Submission call sequence	Repetition of submission calls of undetermined length
		Chatter call sequence	Repetition of chatter calls of undetermined length
		Moving call sequence	Repetition of moving calls of undetermined length
		Short call sequence (sc.>4)	Repetition of more than 4 short calls
	Finite	2 short calls (sc.2)	Repetition of 2 short calls
		3 short calls (sc.3)	Repetition of 3 short calls
		4 short calls (sc.4)	Repetition of 4 short calls
		Quasi-combination (qc)	Repetition of 2 short calls with no silence between them
Mixed call combinations	Graded	Food aggression sequence	Two acoustically different aggression calls grading into each other with intermediate calls, likely related to low and high arousal
	Discrete	Di-drrr calls	A short call followed by a longer wheek call, potentially with modulation
		Mixed short call sequence (sc+)	Sequence containing a short call and one or two quasi-combinations or di-drrr calls
		Long sequence	Sequence containing 3 or more calls and at least two different call types

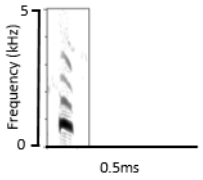
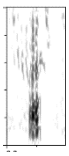
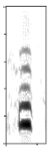
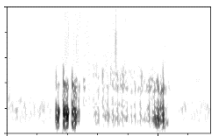
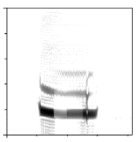
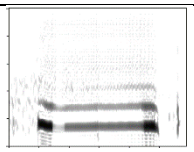
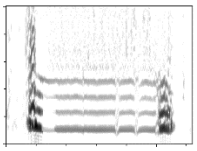
The eight other call combination types were produced in more than one behavioural context. Whilst longer 'short call sequences' (sc.>4), 'mixed short call sequences' (sc+) and 'quasi-combinations' (qc) were never produced in the digging context the remaining call combinations (sc.2, 'three short calls' (sc.3), 'four short calls' (sc.4), long sequences and 'di-drrr calls') were produced in all contexts. The proportions of specific call combinations emitted in relation to the total number of call combinations produced varied with context: this was the case for sc.2 (GLMM, df=5, χ^2=17, p=0.005, p_{adj}=0.013), sc.4 (GLMM, df=5, χ^2=13, p=0.024, p_{adj}=0.048), di-drrr calls (GLMM, df=5, χ^2=19, p=0.002, p_{adj}=0.008) and long sequences (GLMM, df=5, χ^2=19, p=0.002, p_{adj}=0.008) (see table 4 and figure 2). Meerkats produced a lower proportion of sc.2 and a higher proportion of long sequences in the moving context than in any other context (see table 4). Sc.2, the most frequently produced combination, was given in higher proportions in the vigilance and sunning contexts. Di-drrr combinations were produced in higher proportions in the babysitting, moving and digging contexts.

Long Sequences

Long sequences, whose component calls include 'short calls' (sc), qc, di-drrr calls, 'lead calls' and 'moving calls', were produced by meerkats in six out of the eight contexts, with the majority produced in the moving context (131/194). Of the 194 long sequences produced, few were emitted in the digging and relaxed contexts (recorded 2 and 5 times respectively) and so these contexts were excluded from the analysis. Five other sequences were not of sufficient quality to identify the calls composing them. In total 182 long sequences were of high enough quality to include in the analysis. No long sequences were produced in the aggression and submission contexts

The length (number of calls) of long sequences varied with the context (GLMM, df=3, χ^2=9, p=0.035) (see figure 3). Long sequences contained the most calls when produced in moving contexts (10±0.6) and the fewest calls when produced in babysitting contexts (5.3±0.6). We found no significant difference in number of calls in the long sequences between sunning (7.9±1.4) and vigilance (6.6±0.9) contexts.

Table 3: Description of the main call types comprising meerkat call combinations and the contexts they are produced in. The time and frequency scales apply to all spectrograms.

Call type	Spectrogram	Context	Reference
Short call		Vigilance and social interactions (sunning and allogrooming)	Manser, 1998, 1999
Chatter call		Play fighting, defending	Manser, 1998
Submission call		Submission	Manser, 1998
Aggression call		Food competition	Manser, 1998
Wheek call		Vigilance	Manser, 1998, 1999
Moving call		Foraging, moving between food patches	Bousquet, Sumpter, & Manser, 2010
Lead calls		Moving (leaving sleeping burrow, after an alarm, moving between food patches)	Bousquet et al., 2010

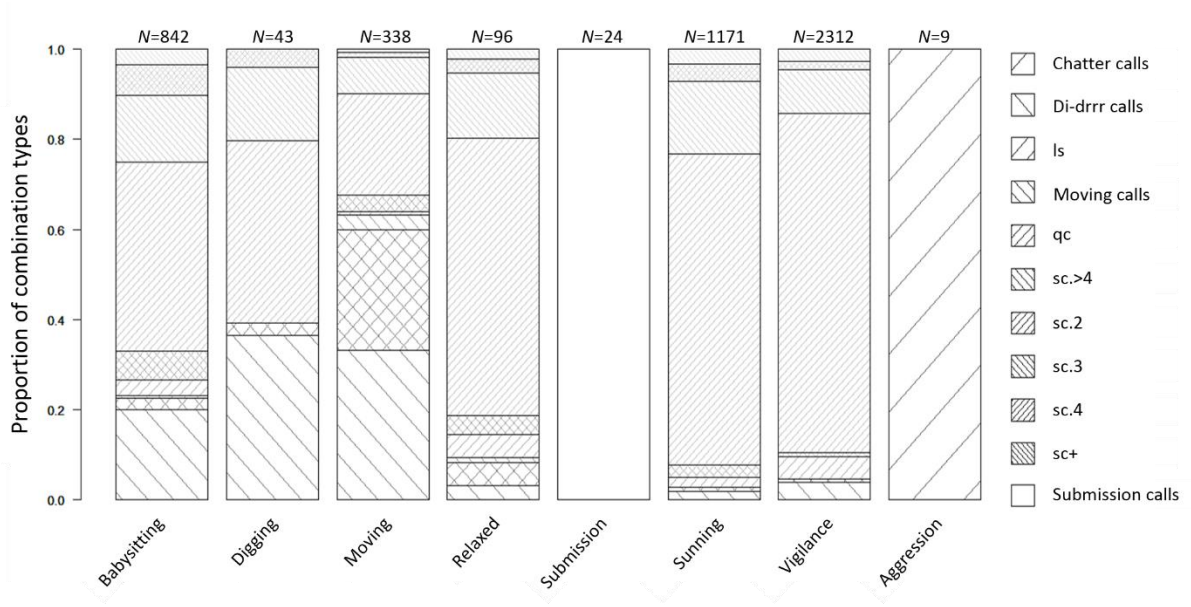


Figure 2: Proportions of the eleven different call combination types collected in the two-month field period in the eight different behavioural contexts. ls: long sequence; qc: quasi-combination; sc.>4: short call sequence; sc.2: two short calls; sc.3: three short calls; sc.4: four short calls; sc+: mixed short call sequence. N indicates the number of combinations recorded in a context.

Investigating the call types that initiated long sequences, we found that only the proportion of long sequences starting with a di-drrr call varied with context (GLMM, df=3, χ^2=14, p=0.002, p_{adj}=0.01). Specifically, there was a higher proportion of long sequences initiated by a di-drrr call in the babysitting context (14/28) than in the other contexts. A lower proportion of long sequences started with a di-drrr call in the moving and vigilance contexts (respectively 24/126 and 1/18), and no long sequences started with a di-drrr call in the sunning context (0/10). The proportion of long sequences starting with the other call types did not vary between contexts (GLMM, sc: df=3, χ^2=4, p=0.3, p_{adj}=0.3; lead calls: df=3, χ^2=6, p=0.1, p_{adj}=0.3; moving call: df=3, χ^2=4, p=0.3, p_{adj}=0.3; qc: df=3, χ^2=4, p=0.2, p_{adj}=0.3).

The proportions of sc within a long sequence varied with context (GLMM, df=3, χ^2=11, p=0.010, p_{adj}=0.050) (see figure 4). Long sequences produced in the moving context consisted of a lower proportion of sc than the sunning contexts. We found no significant difference in the proportion of the other call types in long sequences between contexts (GLMM, di-drrr: df=3, χ^2=6, p=0.10, p_{adj}=0.17; lead call: df=3, χ^2=8, p=0.04, p_{adj}=0.10; moving calls: df=3, χ^2=3, p=0.40, p_{adj}=0.40; qc: df=3, χ^2=3, p=0.32, p_{adj}=0.40).

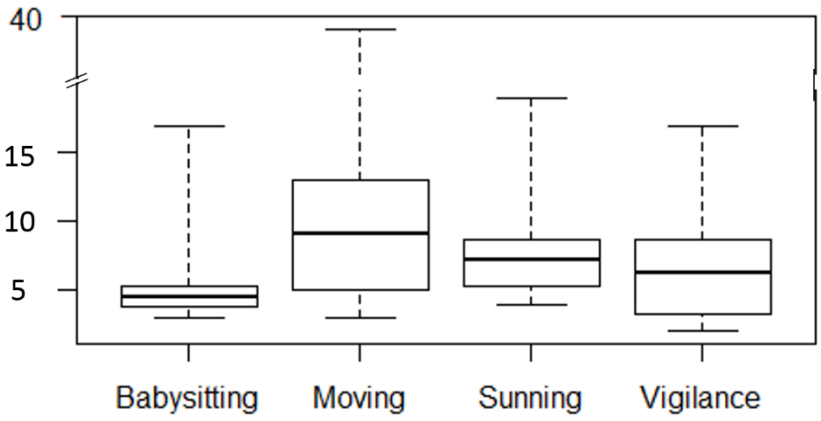


Figure 3: Length of long sequences, in number of component calls, produced in different behavioural contexts. Boxplot shows the median, interquartiles and range.

Figure 4: Mean proportions of the different call types composing long sequences produced in different behavioural contexts.

Table 4: Comparison of the proportions of call combination types produced in different behavioural contexts. ↑: higher proportion; ↓: lower proportion; NS: Non-significant difference; —: combination type not produced in this context. p-values adjusted using false discovery rate. sc.2: two short calls; sc.3: three short calls; sc.4: four short calls; sc.>4: short call sequence; sc+: mixed short call sequence; qc: quasi-combinations; ls: long sequence.

		Sunning	Relaxed	Babysitting	Digging	Moving	Vigilance
Sunning	sc.2		↑ than relaxed; p=0.040	↑ than babysitting; p=0.055	↑ than digging; p=0.035	↑ than moving; p<0.001	NS; p=0.945
	sc.3		NS overall	NS overall	NS overall	NS overall	NS overall
	sc.4		NS; p=0.746	NS; p=0.746	NS; p=0.746	NS; p=0.288	NS; p=0.283
	sc.>4		NS overall	NS overall	—	NS overall	NS overall
	sc+		NS overall	NS overall	—	NS overall	NS overall
	qc		NS overall	NS overall	—	NS overall	NS overall
	di-drrr		NS; p=0.423	↓ than babysitting; p=0.044	↓ than digging; p<0.001	↓ than moving; p<0.001	NS; p=0.521
	ls		NS; p=0.547	NS; p=0.284	NS; p=0.547	↓ than moving; p<0.001	NS; p=0.252
Relaxed	sc.2	↓ than sunning; p=0.040		NS; p=0.687	NS; p=0.671	↑ than moving; p=0.001	↓ than vigilance; p=0.055
	sc.3	NS overall		NS overall	NS overall	NS overall	NS overall
	sc.4	NS; p=0.746		NS; p=0.680	NS; p=0.735	NS; p=0.680	NS; p=0.680
	sc.>4	NS overall		NS overall	—	NS overall	NS overall
	sc+	NS overall		NS overall	—	NS overall	NS overall
	qc	NS overall		NS overall	—	NS overall	NS overall
	di-drrr	NS; p=0.423		NS; p=0.209	NS; p=0.142	NS; p=0.142	NS; p=0.343
	ls	NS; p=0.912		NS; p=0.245	NS; p=0.114	↓ than moving; p=0.012	NS; p=0.249
Baby -sitting	sc.2	↓ than sunning; p=0.035	NS; p=0.687		NS; p=0.441	↑ than moving; p<0.001	↓ than vigilance; p=0.072
	sc.3	NS overall	NS overall		NS overall	NS overall	NS overall
	sc.4	NS; p=0.757	NS; p=0.741		NS; p=0.912	NS; p=0.283	NS; p=0.283
	sc.>4	NS overall	NS overall		—	NS overall	NS overall
	sc+	NS overall	NS overall		—	NS overall	NS overall
	qc	NS overall	NS overall		—	NS overall	NS overall
	di-drrr	↑ than sunning; p=0.039	NS; p=0.209		NS; p=0.151	NS; p=0.142	NS; p=0.098
	ls	NS; p=0.275	NS; p=0.514		NS; p=0.483	↓ than moving; p=0.011	↑ than vigilance; p=0.065

		Sunning	Relaxed	Babysitting	Digging	Moving	Vigilance
Digging	sc.2	↓ than sunning; p=0.035	NS; p=0.671	NS; p=0.441		↑ than moving; p=0.035	↓ than vigilance; p=0.030
	sc.3	NS overall	NS overall	NS overall		NS overall	NS overall
	sc.4	NS; p=0.680	NS; p=0.680	NS; p=0.800		NS; p=0.283	NS; p=0.283
	sc.>4	—	—	—		—	—
	sc+	—	—	—		—	—
	qc	—	—	—		—	—
	di-drrr	↑ than sunning; p<0.001	NS; p=0.142	NS; p=0.151		NS; p=0.734	↑ than vigilance; p<0.001
	ls	NS; p=0.384	NS; p=0.657	NS; p=0.241		↓ than moving; p=0.012	NS; p=0.976
Moving	sc.2	↓ than sunning; p<0.001	↓ than relaxed; p=0.001	↓ than babysitting; p=0.001	↓ than digging; p=0.038		↓ than vigilance; p<0.001
	sc.3	NS overall	NS overall	NS overall	NS overall		NS overall
	sc.4	NS; p=0.366	NS; p=0.680	NS; p=0.283	NS; p=0.396		NS; p=0.997
	sc.>4	NS overall	NS overall	NS overall	—		NS overall
	sc+	NS overall	NS overall	NS overall	—		NS overall
	qc	NS overall	NS overall	NS overall	—		NS overall
	di-drrr	↑ than sunning; p<0.001	NS; p=0.160	NS; p=0.142	NS; p=0.722		↑ than vigilance; p<0.001
	ls	↑ than sunning; p<0.001	NS; p=0.126	↑ than babysitting; p=0.059	NS; p=0.284		↑ than vigilance; p=0.005
Vigilance	sc.2	NS; p=0.945	↑ than relaxed; p=0.055	NS; p=0.209	↑ than digging; p=0.030	↑ than moving; p<0.001	
	sc.3	NS overall	NS overall	NS overall	NS overall	NS overall	
	sc.4	NS; p=0.243	NS; p=0.680	NS; p=0.201	NS; p=0.283	NS; p=0.746	
	sc.>4	NS overall	NS overall	NS overall	—	NS overall	
	sc+	NS overall	NS overall	NS overall	—	NS overall	
	qc	NS overall	NS overall	NS overall	—	NS overall	
	di-drrr	NS; p=0.428	NS; p=0.324	NS; p=0.119	↓ than digging; p<0.001	↓ than moving; p<0.001	
	ls	NS; p=0.321	NS; p=0.920	NS; p=0.114	NS; p=0.912	↓ than moving; p=0.005	

DISCUSSION

In this study we quantified the production of call combinations by wild meerkats in social contexts in order to test the prediction that call combinations should be widespread in such contexts. We first examine call combinations as part of social communication. Secondly, we consider possible mechanisms underlying call combination production. Thirdly, we compare call combination use in social and predation contexts. Finally, we discuss potential implications of this study for research into human language evolution.

Call Combinations as part of Social Communication

In this study, we have shown that meerkats produce twelve different types of call combinations from seven discrete call types and call combinations were emitted across all of the eight main social contexts. This frequent and broad occurrence implies that call combinations represent a non-negligible part of social communication for this species. These results fall in line with previous research in some primate species for which high rates of call combination production overall were also shown. For example 49% of chimpanzee calls (Crockford & Boesch, 2005) and 38% of wedge-capped capuchin (*Cebus olivaceus*) calls were produced in combinations (Robinson, 1984).

We identified call combinations produced in social contexts that fitted the definitions of the two main categories of combination: repetitions of the same call type and mixed call combinations, comprising several discrete call types. Repetitions, containing only one call type, differed from one another either in terms of the call type repeated (e.g. chatter calls vs short calls) or by the number of repetitions (e.g. within short call sequences: sc.2 vs sc.3). Mixed call combinations likewise differed in component call types (for example, di-drrr calls comprise two distinct call types, a short call and a wheek call whereas call sequences in the context of food competition comprised various gradations of aggression calls). Mixed call combinations also showed more variation within a combination type, for example individual long sequences differed in component calls, number of calls and call order. Additionally, some long sequences seemed to have a higher structural complexity with combinations embedded inside other combinations, such as long sequences including di-drrr calls, which are themselves mixed combinations (see above).

Structurally complex combinations that include other combinations have been observed in the closely related banded mongoose. Specifically, banded mongooses can combine their close

calls with distinct, additional calls producing new combinations in three contexts: leading the group, lost from the group or in excitement at rain or wet ground (Jansen, 2013). The close calls themselves are composed of two acoustic segments, an initial noisy segment and a second harmonic segment. Acoustic analysis has shown that the initial noisy part carries information about the caller's identity whereas the second harmonic part carries information about the caller's activity (Jansen et al., 2012). Hence, in these combinations, banded mongoose could potentially indicate the caller's identity, its activity and an external event such as the beginning of rain. However, so far it has not been tested what information receivers actually extract from such a combination. In line with this, we have yet to investigate what information receivers extract from call combinations, and in particular from long sequences, in meerkats. One possibility is that more complex combinatorial structures encode a greater variety of information. However, in some cases, the variation in complexity itself may carry information, regarding, for example, the caller's quality, as is the case in European starling (*Sturnus vulgaris*) song (Mountjoy & Lemon, 1991).

The fact that combinations of similar structural complexity are found in two closely related mongoose species could indicate that combinatorial tendency per se is a shared trait inherited through common descent. However, these species also share similarities in their social structure, both being group living, cooperative breeders, albeit with meerkats having a more despotic hierarchy (Manser et al., 2014). This social structure may have favoured the production of call combinations in these species given that it has been hypothesized that new inferential processes evolve when communication is driven by more cooperative motives (Vygotsky, 1980 cited by Pika & Bugnyar, 2011). Comparative analyses of the communication systems of species from different taxa and/or social systems are needed to shed light on the evolution of communicative complexity and combinatoriality which could in turn help disentangle these two alternative possibilities.

Mechanisms of Call Combination Production

Through systematically documenting the structural variance underlying sequences of calls, our work suggests there may be two primary combinatorial operations that guide meerkat call combination production. The first is where each individual call within the combination is associated with the caller's internal state and the caller emits these calls sequentially as the situation unfolds. The resulting call combinations could therefore reflect the persistence of a

single internal state of the caller, as is probably the case for unlimited repetitions such as meerkat submission or chatter call sequences. Alternatively, the call combinations could reflect the caller's changing internal states, potentially induced by changes in external events (e.g. approach of a rival), which can emerge in two ways. Firstly, the change in internal state could be due to variations in emotion, in particular arousal. For example, in graded food aggression call sequences, the individual calls can reflect varying levels of aggression, where the motivation stays the same, but the arousal changes. Secondly, the change in internal state leading to the production of a call combination could be linked to varying motivations. In meerkats, long sequences may be an example of such a combination with the different component calls reflecting different motivations, though this remains to be tested. The production of combinations linked to differing motivations has been reported in several primate species (Cleveland & Snowdon, 1982; Robinson, 1984; Crockford & Boesch, 2005; Rothacher, 2013) where combinations are produced in contexts intermediate to those of the individual component calls. The production of such call combinations that might depend on internal state could be argued to rely on relatively simple proximate mechanisms and our work suggests that changes in arousal could lead to the use of graded mixed call combinations whereas changes in motivation could lead to the use of discrete mixed call combinations.

The second combinatorial operation by which other call combinations seem to be produced is less flexible. In these combinations the component calls cannot be freely combined, they always appear in a stereotyped order and/or number of occurrences. One example of such a combination from our data set would be the di-drrr calls which always consisted of a short call followed by a wheek call, with call order and call number remaining unchanged for all of the 530 exemplars recorded. Such call combinations do not seem to be the result of changing or conflicting internal states but may reflect a particular consistent internal state or external event.

To determine which of these two mechanisms is used for the production of a combination, callers could be observed in situations leading either to i) varying levels of arousal or to ii) several motivations. One could then record if the individual component calls reflect the immediate arousal or the motivational state of the caller or, rather, if they are always emitted in a stereotyped order. Documenting the proximate mechanisms by which calls come to be associated with other calls is particularly important as it will lead to a better understanding of the evolutionary scenario accompanying the emergence of combinatoriality in general.

Social vs Predation Contexts

When analysing social call combinations, we noticed certain similarities with call combinations produced in predatory contexts. Specifically, meerkats emit three of the combination classes in both contexts: unlimited repetitions, graded and discrete mixed call combinations. Unlimited repetitions in social contexts, such as submission or chatter call sequences, seem to have the same function as those produced in predation contexts, such as bark call sequences (Manser et al., 2014; Townsend et al., 2014): to indicate the persistence of a state either internal or external of the signaller. In the case of graded mixed call combinations, graded alarm call sequences seem to be produced in a similar way to food aggression call sequences with the variation in structure of the calls reflecting a change in the caller's arousal, here in terms of alertness or aggressiveness respectively. However, the discrete mixed call combinations in the social and predation situations seem to present some differences. This type of combination in social contexts seems to either be produced as a single unit such as the di-drrr call or perhaps, in the case of the long sequences, may reflect the caller's multiple or conflicted motivations. On the other hand, in the terrestrial-moving animal sequence meerkats produce sequences of terrestrial alarm calls and moving animal calls, normally given to moving animals regardless of whether they are dangerous or not, in response to moving terrestrial predators (Manser, 2009; Manser et al., 2014). This sequence combines two functionally referential calls to produce a new meaning derived from the meaning of the component calls. It is possible to compare this combination with a simple two-expression package akin to those seen in early developing languages or when children initiate their syntactic development (Hurford, 2011). This sequence could therefore be considered as a more syntax-like combination, where syntax is the level of combinatoriality in which meaningful morphemes or words are combined into larger structures such as sentences in human language (de Boer, Sandler, & Kirby, 2012). Lastly, finite repetitions seem to be a class of combinations specific to social contexts in meerkats as they are not found in predation contexts (Manser et al., 2014). Thus, whilst meerkats do seem to produce more classes of combinations in social contexts as opposed to predation contexts, at present, they do not seem to produce meaningful syntax-like combinations in the former.

Meerkat call combinations in the social context could be argued to surpass those in predatory contexts in variety, both in classes and complexity. This would seem to support the hypothesis that social contexts are important in selecting for combinations because of the variety of behaviours and interactions they involve that are coordinated by vocalisations (Collier et al., 2014). In line with this, previous modelling work has indicated that when behaviours and

interactions outweigh the number of discrete vocalisations in the species vocal repertoire one solution to this pressure involves the concatenation of calls (Nowak et al., 2000). The extent to which social and ecological pressures contribute to promoting combinatoriality requires further work, though comparisons with other species, particularly in terms of the forms sequences take in social and ecological contexts, is one valuable way to do this.

Despite apparent differences in terms of types and complexity of call combinations emitted in social and predation contexts, meerkats seem to produce an arguably more syntax-like combination in the predation but not social context. Other well-known examples of syntax-like call combinations, such as Campbell monkey alarm calls (Ouattara et al., 2009), are also produced in a predation context. It therefore appears that certain combinations in predation contexts seem to be, at least on the surface level, more similar to human forms of combinatoriality than those produced in social situations. Given the survival benefits associated with efficiently transferring more specific information in dangerous contexts, it could be hypothesised that alarm contexts may select for less ambiguous (and hence referential) sequences. Deconstructing the meaning of the combination as a function of the meaning of the individual calls may then be easier compared to combinations composed of non-referential calls which could, in turn, lead to a bias in identifying syntax-like combinations in predation as opposed to social contexts. Whilst these considerations should be taken into account when investigating the form and function of animal call combinations, our data indicates that both social and predation pressures play important roles in the emergence of cognitive abilities facilitating the production and perception of call combinations.

Human Language Evolution

Comparative studies looking at call combinations in animal communication systems are one method of exploring the evolution of language and in particular its combinatorial layers, phonology and syntax. These forms of articulation have received renewed empirical interest over the years given that they are fundamental in facilitating the creation of a large lexicon out of relatively few sounds: a central feature of human language (Hockett, 1960; Hurford, 2008; Hurford, 2011). An increased focus on call combinations, particularly in social contexts may reveal combinations to be more widespread in animal vocal communication than previously documented. However, in meerkats it is worth noting that the production of at least some of these combinations seems to result from simple mechanisms far removed from the complexity

of human syntax. Whilst in meerkats, combinations in predation contexts might be more syntax-like and therefore afford better opportunities for comparative research, studying more "primitive" social combinations could also help better understand, at the proximate level, how combinations emerge in the first place.

Conclusion

In conclusion, meerkats frequently use call combinations across a wide variety of social contexts. Although several classes of combination are found in both social and predation contexts, there seems to be more classes of combinations, some of which present a higher complexity, in the social situations. Whilst animal call combinations have been often described in alarm contexts, our study on meerkats indicates that social contexts are at least as important for the study of call combinations in animal communication as predation contexts. Future research needs to complement our findings by investigating exactly how receivers perceive social call combinations in meerkats in order to fully identify the function of call combinations in animal communication.

Combinatoriality is one way by which information output can be increased in spite of a limited number of signals. Despite its importance, particularly in the case of vocal communication, little is known about the pressures that select for combinatoriality. Further research on call combinations between and across species and contexts is necessary to shed more light on how and why combinatoriality emerged.

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Supplementary Table A1: Meerkat calls and the contexts they are produced in according to Manser (1998).

Context	Call	Single/Multiple element	Discrete/Graded
Spatial coordination	Close call	Single	Discrete
	Joining call	Multiple	Discrete
	Leading call	Single/Multiple	Graded
	Lost call	Single	Discrete
	Moving call	Single/Multiple	Graded
Social interaction	Aggression call	Single/Multiple	Graded
	Chatter call	Multiple	Discrete
	Grooming call	Single/Multiple	Discrete
	Submissive call	Multiple	Discrete
Social interaction & sentinel duty	Single note call	Single	Discrete
Sentinel duty	Di-drrr call	Multiple	Discrete
	Double note call	Multiple	Discrete
	Triple note call	Multiple	Discrete
	Multiple note call	Multiple	Discrete
	Wheek call	Single	Discrete
Alarm call	Aerial alarm call	Single/Multiple	Graded
	High Pitched barking	Single/Multiple	Discrete
	Moderate alarm call	Single/Multiple	Graded
	Panic call	Single	Graded
	Recruitment call	Single/Multiple	Graded
	Rolling alarm call	Single	Graded
	Spitting call	Single/Multiple	Discrete
	Terrestrial alarm call	Single/Multiple	Graded
	Worry call	Single/Multiple	Graded
Alarm call & spatial coordination	Barking call	Single/Multiple	Discrete
Calls given by pups	Begging call (pup)	Single/Multiple	Graded
	Chatter call (pup)	Single/Multiple	Discrete
	Digging call (pup)	Single	Graded
	Eating call (pup)	Single	Graded
	Excited call (pup)	Multiple	Graded
	Joining call (pup)	Multiple	Discrete
	Lost call (pup)	Single	Discrete
	Moving off call (pup)	Multiple	Discrete
	Sleeping call (pup)	Single	Discrete
	spitting call (pup)	Single/Multiple	Discrete

Following Catchpole & Slater (2003) an element is defined as a continuous trace on a spectrograph.

Supplementary Table A2: Number of times each combination type was recorded during the two-month study Period.

Combination	Occurrence
Submission call sequence	24
Chatter call sequence	9
Moving call sequence	22
sc.>4	150
sc.2	3361
sc.3	666
sc.4	178
qc	198
Di-drrr	530
Food aggression call sequence	0
sc+	149
Long sequence	195

REFERENCES

Altmann, J. (1974). Observational study of behavior: sampling methods. *Behaviour*, *49*(3), 227–266. doi: 10.1163/156853974X00534

Arnold, K., & Zuberbühler, K. (2006). Language evolution: Semantic combinations in primate calls. *Nature*, *441*(7091), 303–303. doi: 10.1038/441303a

Arnold, K., & Zuberbühler, K. (2012). Call combinations in monkeys: Compositional or idiomatic expressions? *Brain and Language*, *120*(3), 303–309. doi: 10.1016/j.cub.2008.01.040

Baayen, R. H. (2008). *Analyzing linguistic data: A practical introduction to statistics using R*. Cambridge, UK: Cambridge University Press.

Bates D, Maechler M, Bolker B and Walker S (2015). lme4: Linear mixed-effects models using Eigen and S4_. R package version 1.1-8, URL: http://CRAN.R-project.org/package=lme4>.

Benjamini, Y., & Hochberg, Y. (1995). Controlling the false discovery rate: A practical and powerful approach to multiple testing. *Journal of the Royal Statistical Society. Series B (Methodological)*, *57*(1), 289–300.

Blumstein, D. T., & Armitage, K. B. (1997). Alarm calling in yellow-bellied marmots: I. The meaning of situationally variable alarm calls. *Animal Behaviour*, *53*(1), 143–171. doi: 10.1006/anbe.1996.0285

Bouchet, H., Pellier, A.-S., Blois-Heulin, C., & Lemasson, A. (2010). Sex differences in the vocal repertoire of adult red-capped mangabeys (*Cercocebus torquatus*): a multi-level acoustic analysis. *American Journal of Primatology*, *72*(4), 360–375. doi: 10.1002/ajp.20791

Bousquet, C. A. H., Sumpter, D. J. T., & Manser, M. B. (2010). Moving calls: A vocal mechanism underlying quorum decisions in cohesive groups. *Proceedings of the Royal Society B: Biological Sciences*, *278*(1711), 1482–1488. doi: 10.1098/rspb.2010.1739

Briefer, E. F. (2012). Vocal expression of emotions in mammals: mechanisms of production and evidence: Vocal communication of emotions. *Journal of Zoology*, *288*(1), 1–20. doi: 10.1111/j.1469-7998.2012.00920.x

Candiotti, A., Zuberbühler, K., & Lemasson, A. (2012). Context-related call combinations in female Diana monkeys. *Animal Cognition*, *15*(3), 327–339. doi: 10.1007/s10071-011-0456-8

Cäsar, C., Byrne, R. W., Young, R. J., & Zuberbühler, K. (2012). The alarm call system of wild black-fronted titi monkeys, *Callicebus nigrifrons*. *Behavioral Ecology and Sociobiology*, *66*(5), 653–667. doi: 10.1007/s00265-011-1313-0

Clarke, E., Reichard, U. H., & Zuberbühler, K. (2006). The syntax and meaning of wild gibbon songs. *PLoS One*, *1*(1), e73. doi: 0.1371/ journal.pone.0000073

Clay, Z., & Zuberbühler, K. (2009). Food-associated calling sequences in bonobos. *Animal Behaviour*, *77*(6), 1387–1396. doi: 10.1016/j.anbehav.2009.02.016

Cleveland, J., & Snowdon, C. T. (1982). The complex vocal repertoire of the adult cotton-top tamarin (*Saguinus oedipus oedipus*). *Zeitschrift Für Tierpsychologie*, *58*(3), 231–270. doi: 10.1111/j.1439-0310.1982.tb00320.x

Clutton-Brock, T. H., Gaynor, D., Kansky, R., MacColl, A. D. C., McIlrath, G., Chadwick, P., … Skinner, J. D. (1998). Costs of cooperative behaviour in suricates (*Suricata suricatta*). *Proceedings of the Royal Society B: Biological Sciences*, *265*(1392), 185–190. doi: 10.1098/rspb.1998.0281

Clutton-Brock, T. H., Hodge, S. J., Spong, G., Russell, A. F., Jordan, N. R., Bennett, N. C., … Manser, M. B. (2006). Intrasexual competition and sexual selection in cooperative mammals. *Nature*, *444*(7122), 1065–1068. doi: 10.1038/nature05386

Collier, K., Bickel, B., van Schaik, C. P., Manser, M. B., & Townsend, S. W. (2014). Language evolution: syntax before phonology? *Proceedings of the Royal Society B: Biological Sciences*, *281*(1788). doi: 10.1098/rspb.2014.0263

Crockford, C., & Boesch, C. (2005). Call combinations in wild chimpanzees. *Behaviour*, *142*(4), 397–421. doi: 10.1163/1568539054012047

Darwin, C. (1872). *The Expression of the Emotions in Man and Animals* (Original edition). London: Penguin Classics.

de Boer, B., Sandler, W., & Kirby, S. (2012). New perspectives on duality of patterning: Introduction to the special issue. *Language and Cognition*, *4*(4), 251–259. doi: 10.1515/langcog-2012-0014

delBarco-Trillo, J., Greene, L. K., Goncalves, I. B., Fenkes, M., Wisse, J. H., Drewe, J. A., … Drea, C. M. (2016). Beyond aggression: Androgen-receptor blockade modulates social interaction in wild meerkats. *Hormones and Behavior*, *78*, 95–106. doi: 10.1016/j.yhbeh.2015.11.001

Doolan, S. P., & Macdonald, D. W. (1996). Diet and foraging behaviour of group-living meerkats, *Suricata suricatta*, in the southern Kalahari. *Journal of Zoology*, *239*(4), 697–716. doi: 10.1111/j.1469-7998.1996.tb05472.x

Engesser, S., Crane, J. M. S., Savage, J. L., Russell, A. F., & Townsend, S. W. (2015). Experimental Evidence for Phonemic Contrasts in a Nonhuman Vocal System. *PLOS Biology*, *13*(6), e1002171. doi: 10.1371/journal.pbio.1002171

Fitch, W. T. (2000). Skull dimensions in relation to body size in nonhuman mammals: The causal bases for acoustic allometry. *Zoology-Analysis of Complex Systems*, *103*(1–2), 40–58.

Freeberg, T. M., Dunbar, R. I. M., & Ord, T. J. (2012). Social complexity as a proximate and ultimate factor in communicative complexity. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, *367*(1597), 1785–1801. doi: 10.1098/rstb.2011.0213

Habicher, A. (2009). *Behavioural cost minimisation and minimal invasive blood-sampling in meerkats (*S. suricatta, Herpestidae*)*. (PhD). University of Köln, Köln, Germany.

Harrison, X. A. (2014). Using observation-level random effects to model overdispersion in count data in ecology and evolution. *PeerJ*, *2*, e616. doi: 10.7717/peerj.616

Hedwig, D., Mundry, R., Robbins, M. M., & Boesch, C. (2014). Contextual correlates of syntactic variation in mountain and western gorilla close-distance vocalizations: Indications for lexical or phonological syntax? *Animal Cognition*. doi: 10.1007/s10071-014-0812-6

Hockett, C. F. (1960). The origin of speech. *Scientific American*, *203*, 88–111.

Hurford, J. R. (2008). The evolution of human communication and language. In P. D'Ettorre & D. P. Hughes (Eds.), *Sociobiology of communication: An interdisciplinary perspective* (pp. 249–264). Oxford, UK: Oxford University Press.

Hurford, J. R. (2011). *The origins of grammar: Language in the light of evolution II* (Vol. 2). Oxford, UK: Oxford University Press.

Jackendoff, R. (1999). Possible stages in the evolution of the language capacity. *Trends in Cognitive Sciences*, *3*(7), 272–279. doi: 10.1016/S1364-6613(99)01333-9

James, P. C., & Robertson, H. A. (1985). The call of Bulwer's Petrel (*Bulweria bulwerii*), and the relationship between intersexual call divergence and aerial calling in the nocturnal Procellariiformes. *The Auk*, *102*(4), 878–882.

Jansen, D. A. W. A. M. (2013). *Vocal communication in the banded mongoose* (PhD). University of Zurich, Zurich, Switzerland.

Jansen, D. A. W. A. M., Cant, M. A., & Manser, M. B. (2012). Segmental concatenation of individual signatures and context cues in banded mongoose (*Mungos mungo*) close calls. *BMC Biology*, *10*(1), 97. doi: 10.1186/1741-7007-10-97

Jordan, N. R., Cherry, M. I., & Manser, M. B. (2007). Latrine distribution and patterns of use by wild meerkats: implications for territory and mate defence. *Animal Behaviour*, *73*(4), 613–622. doi: 10.1016/j.anbehav.2006.06.010

Keenan, S., Lemasson, A., & Zuberbühler, K. (2013). Graded or discrete? A quantitative analysis of Campbell's monkey alarm calls. *Animal Behaviour*, *85*(1), 109–118. doi: 10.1016/j.anbehav.2012.10.014

Kershenbaum, A., Blumstein, D. T., Roch, M. A., Akçay, Ç., Backus, G., Bee, M. A., … Zamora-Gutierrez, V. (2014). Acoustic sequences in non-human animals: a tutorial review and prospectus. *Biological Reviews*. doi: 10.1111/brv.12160

Landis, J. R., & Koch, G. G. (1977). The measurement of observer agreement for categorical data. *Biometrics*, 159–174. doi: 10.2307/2529310

Lemasson, A., Ouattara, K., Bouchet, H., & Zuberbühler, K. (2010). Speed of call delivery is related to context and caller identity in Campbell's monkey males. *Naturwissenschaften*, *97*(11), 1023–1027. doi: 10.1007/s00114-010-0715-6

Macedonia, J. M. (1990). What is communicated in the antipredator calls of lemurs: evidence from playback experiments with ringtailed and ruffed lemurs. *Ethology*, *86*(3), 177–190. doi: 10.1111/j.1439-0310.1990.tb00428.x

Macedonia, J. M., & Evans, C. S. (1993). Essay on contemporary issues in ethology: Variation among mammalian alarm call systems and the problem of meaning in animal signals. *Ethology*, *93*(3), 177–197. doi: 10.1111/j.1439-0310.1993.tb00988.x

Manser, M. B. (1998). *The evolution of auditory communication in suricates*, Suricata suricatta. (PhD). University of Cambridge, Cambridge, UK.

Manser, M. B. (1999). Response of foraging group members to sentinel calls in suricates, *Suricata suricatta*. *Proceedings of the Royal Society B: Biological Sciences*, *266*(1423), 1013–1019. doi: 10.1098/rspb.1999.0737

Manser, M. B. (2001). The acoustic structure of suricates' alarm calls varies with predator type and the level of response urgency. *Proceedings of the Royal Society B: Biological Sciences*, *268*(1483), 2315–2324. doi: 10.1098/rspb.2001.1773

Manser, M. B. (2009). What Do Functionally Referential Alarm Calls Refer To? In *Cognitive ecology II* (pp. 229–246). Chicago, IL, USA: University of Chicago Press.

Manser, M. B., & Bell, M. B. (2004). Spatial representation of shelter locations in meerkats, *Suricata suricatta*. *Animal Behaviour*, *68*(1), 151–157. doi: 10.1016/j.anbehav.2003.10.017

Manser, M. B., Bell, M. B., & Fletcher, L. B. (2001). The information that receivers extract from alarm calls in suricates. *Proceedings of the Royal Society B: Biological Sciences*, *268*(1484), 2485–2491. doi: 10.1098/rspb.2001.1772

Manser, M. B., Jansen, D. A. W. A. M., Graw, B., Hollén, L. I., Bousquet, C. A. H., Furrer, R. D., & le Roux, A. (2014). Vocal complexity in meerkats and other mongoose species. In *Advances in the Study of Behavior* (Vol. 46, pp. 281–310). Elsevier.

Manser, M. B., Seyfarth, R. M., & Cheney, D. L. (2002). Suricate alarm calls signal predator class and urgency. *Trends in Cognitive Sciences*, *6*(2), 55–57. doi: 10.1016/S1364-6613(00)01840-4

Marler, P. (1976). Social organization, communication and graded signals: The chimpanzee and the gorilla. In *Growing Points in Ethology*. Cambridge, UK: Cambridge University Press.

Morton, E. S. (1977). On the occurrence and significance of motivation-structural rules in some bird and mammal sounds. *The American Naturalist*, *111*(981), 855–869.

Mountjoy, D. J., & Lemon, R. E. (1991). Song as an attractant for male and female European starlings, and the influence of song complexity on their response. *Behavioral Ecology and Sociobiology*, *28*(2), 97–100. doi: 10.1007/BF00180986

Nowak, M. A., & Krakauer, D. C. (1999). The evolution of language. *Proceedings of the National Academy of Sciences*, *96*(14), 8028–8033. doi: 10.1073/pnas.96.14.8028

Nowak, M. A., Krakauer, D. C., & Dress, A. (1999). An error limit for the evolution of language. *Proceedings of the Royal Society of London B: Biological Sciences*, *266*(1433), 2131–2136. doi: 10.1098/rspb.1999.0898

Nowak, M. A., Plotkin, J. B., & Jansen, V. A. A. (2000). The evolution of syntactic communication. *Nature*, *404*(6777), 495–498. doi: 10.1038/35006635

Oller, D. K., & Griebel, U. (2008). *Evolution of communicative flexibility: complexity, creativity, and adaptability in human and animal communication*. Cambridge, Massachusetts, USA: MIT Press.

Ouattara, K., Lemasson, A., & Zuberbühler, K. (2009). Campbell's monkeys use affixation to alter call meaning. *PloS One*, *4*(11), e7808. doi: 10.1371/ journal.pone.0007808

Pika, S., & Bugnyar, T. (2011). The use of referential gestures in ravens (*Corvus corax*) in the wild. *Nature Communications*, *2*, 560. doi: 10.1038/ncomms1567

R Core Team (2015). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL http://www.R-project.org/.

Ręk, P. (2013). Corncrake males learn new signal meanings during aggressive interactions. *Animal Behaviour*, *86*(2), 451–457. doi: 10.1016/j.anbehav.2013.05.042

Robinson, J. G. (1984). Syntactic structures in the vocalizations of wedge-capped capuchin monkeys, *Cebus olivaceus*. *Behaviour*, 46–79. doi: 10.1163/156853984X00551

Rothacher, Y. (2013). *Social call combinations in vervet monkeys* (MSc). University of Zurich, Zurich, Switzerland.

Ryan, M. J. (1980). Female mate choice in a neotropical frog. *Science*, *209*(4455), 523–525.

Schel, A. M., Candiotti, A., & Zuberbühler, K. (2010). Predator-deterring alarm call sequences in Guereza colobus monkeys are meaningful to conspecifics. *Animal Behaviour*, *80*(5), 799–808. doi: 10.1016/j.anbehav.2010.07.012

Schielzeth, H., & Forstmeier, W. (2009). Conclusions beyond support: overconfident estimates in mixed models. *Behavioral Ecology*, *20*(2), 416–420. doi: 10.1093/beheco/arn145

Slater, P. J. B., & Janik, V. M. (2010). Vocal Learning. In Editors-in-Chief: Michael D. Breed & Janice Moore (Eds.), *Encyclopedia of Animal Behavior* (pp. 551–557). Oxford: Academic Press.

Spillmann, B., Dunkel, L. P., van Noordwijk, M. A., Amda, R. N. A., Lameira, A. R., Wich, S. A., & van Schaik, C. P. (2010). Acoustic properties of long calls given by flanged male orang-utans (*Pongo pygmaeus wurmbii*) reflect both individual identity and context. *Ethology*, *116*(5), 385–395. doi: 10.1111/j.1439-0310.2010.01744.x

Townsend, S. W., Charlton, B. D., & Manser, M. B. (2014). Acoustic cues to identity and predator context in meerkat barks. *Animal Behaviour*, *94*, 143–149. doi: 10.1016/j.anbehav.2014.05.021

Vygotsky, L. S. (1980). *Mind in society: The development of higher psychological processes*. Cambridge, Massachusetts, USA: Harvard university press.

Wagner Jr, W. E. (1989). Graded aggressive signals in Blanchard's cricket frog: vocal responses to opponent proximity and size. *Animal Behaviour*, *38*(6), 1025–1038. doi: 10.1016/S0003-3472(89)80141-1

Zimmermann, E. (1985). The vocal repertoire of the adult Senegal bushbaby (*Galago senegalensis senegalensis*). *Behaviour*, *94*(3), 212–233. doi: 10.1163/156853985X00190

CHAPTER 3:

Wild Dwarf Mongooses Produce both Risk Related and Predator-Specific Alarm Calls

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Dwarf mongoose on sentinel on a termite mound.

ABSTRACT

Many species produce alarm calls in response to predator threats. Some are urgency-based, indicating the level of threat perceived, and some are predator-specific, indicating the type of predator attacking. Predator-specific calls are termed functionally referential when they elicit a specific, adaptive, response from the receiver. Differing escape strategies, habitat structural complexity and sociality have been forwarded as factors favouring the evolution of functionally referential calls. Studying closely-related species that differ in either social structure or habitat, such as those belonging to the mongoose family, is one way to investigate the impact of these factors. Baseline information about different species is therefore important for comparative purposes. Captive dwarf mongooses (*Helogale parvula*) have been described as having a sophisticated alarm-call system, transmitting information about predator species, distance and elevation. Using recordings of natural predator encounters, experimental predator presentations and call playbacks, we investigated the alarm-call system of wild dwarf mongooses. We recorded 11 different alarm-call types given to 11 stimulus categories. Three of the five commonly emitted alarm call types appeared to be risk-related whereas the other two seemed to be predator-specific, given to aerial and terrestrial predators respectively. The remaining six were rarely produced. Furthermore, dwarf mongoose aerial alarm calls appear more specific than their terrestrial alarm calls, which are given to both visible terrestrial predators and secondary cues of predators. We discuss this varied alarm-call system and how it compares to those of closely-related species, providing information for future comparative work which may shed light on factors favouring functionally referential alarm calls.

Key-words: *Alarm calls – Dwarf mongoose – Functional reference* – Herpestidae – *Predator-specific – Sociality – Urgency related – Vocal communication*

INTRODUCTION

Many animal species produce vocalisations when detecting predators (Zuberbühler 2006). A key function of such alarm calls is to alert group members to a threat and therefore increase their chances of survival (Marler 1967; Sherman 1977; Stankowich 2010). Alarm calls have been shown to refer to the level of danger a predator represents, as seen in species such as alpine marmots (*Marmota marmota*; Blumstein and Arnold 1995), yellow-bellied marmots (*Marmota flaviventris*: Blumstein and Armitage 1997a), white-browed scrubwrens (*Sericornis frontalis*: Leavesley and Magrath 2005) and banded mongooses (*Mungos mungo*: Furrer & Manser, 2009a). Alarm calls can also be highly predator-specific, given only to a certain category of predator. If predator-specific alarm calls elicit qualitatively distinct behaviours from the receiver that mirror responses shown when encountering different predator types, they are termed functionally referential (Macedonia and Evans 1993). Several species have been shown to give functionally referential alarm calls, with the most often documented being to aerial and terrestrial predators as seen in various primate species (vervet monkeys, *Chlorocebus aethiops*: Struhsaker, 1967; Seyfarth, Cheney, & Marler, 1980; ringtailed lemurs, *Lemur catta*: Macedonia, 1990; Diana monkeys, *Cercopithecus diana*: Zuberbühler, Noë, & Seyfarth, 1997; Campbell monkeys, *Cercopithecus campbelli* : Zuberbühler, 2002; black-fronted titi monkeys, *Callicebus nigrifrons*: Cäsar, Byrne, Hoppitt, Young, & Zuberbühler, 2012; Cäsar, Byrne, Young, & Zuberbühler, 2012). Functionally referential alarm calls can also potentially encode specific features of a predator, including its behaviour (Siberian jays, *Perisoreus infaustus*: Griesser 2008; meerkats, *Suricata suricatta*: Manser et al. 2014), colour (Gunnison's prairie dog, *Cynomys gunnisoni*: Slobodchikoff et al. 2009) and size (Gunnison's prairie dog: Ackers and Slobodchikoff 1999; black-capped chickadee, *Poecile atricapilla*: Templeton et al. 2005). Finally, a single alarm call can refer to both the level of danger and predator type, as shown in meerkats (Manser 2001; Manser et al. 2001).

The need for qualitatively different, incompatible, escape strategies for different predator classes has been suggested as one important factor promoting the production of predator-specific alarm calls (Macedonia 1990). Macedonia and Evans (1993) proposed that habitat, and in particular its structural complexity, may also play a role in favouring such distinct responses and therefore functionally referential alarm calls. For example, ringtailed lemurs, that move both horizontally along the ground and vertically up and down trees, produce functionally referential alarm calls, whereas black and white ruffed lemurs (*Varecia variegata*), that remain primarily in the tree canopy, emit less specific alarm calls (Macedonia and Evans 1993).

However, species such as meerkats and Gunnison's prairie dogs living in less complex, more homogenous habitats, also produce functionally referential alarm calls (Manser 2001; Manser et al. 2001; Slobodchikoff et al. 2009), whereas Cape ground squirrels (*Xerus inauris*), sympatric to meerkats, produce urgency related alarm calls, suggesting a habitat-based explanation is unlikely to be sufficient alone (Furrer and Manser 2009b).

Sociality is an additional factor that has been suggested to promote functionally referential alarm-call systems. Blumstein and Armitage (1997b) have highlighted that more socially complex groups (i.e. those with more complex, kin-structured social systems) could lead to larger alarm-call repertoires and consequently to situationally specific (i.e. both urgency-based and functionally referential) signalling. Whilst it is generally accepted that social and vocal complexity are likely associated (Freeberg et al. 2012), there is no evidence from the marmot studies that social complexity influences the production of functionally referential alarm calls (Blumstein 2007). Yet the comparison between two sympatric group-living species, meerkats and Cape ground squirrels, suggests that the need to coordinate group movement, representing a social constraint, may be an additional factor implicated in triggering the evolution of predator specific alarm calls (Furrer and Manser 2009b).

Ultimately, comparative data are necessary if we are to shed light on the factors promoting the emergence of functionally referential alarm-call systems. Whilst primates have mainly been the focus of such studies, data from a broader taxonomic range would be necessary to help disentangle the relative contribution of various social and ecological factors. Mongooses from the *Herpestidae* family represent an appropriate taxon for such research. These species vary in social systems, ranging from solitary to group-living species, with varying social structures (Manser et al. 2014). Moreover, several African mongoose species of comparable body size face similar predation pressures, being at risk from both large raptors and terrestrial predators (Manser et al. 2014), aiding the exclusion of differences in predation pressure or predator hunting-strategies as potential confounding factors. Furthermore, the fact that some of these species have overlapping distributions but differing social structures (e.g. dwarf mongooses, *Helogale parvula*, and slender mongooses, *Galerella sanguinea*), whilst other species with a similar social structure live in different habitats (e.g. dwarf mongooses and meerkats) (Manser et al. 2014), means the role of the different factors can begin to be disentangled. The alarm-call system of one mongoose species in particular, the meerkat, has been well documented. Meerkats have a sophisticated alarm-call system that rivals that of many primates, including predator-directed (Townsend et al. 2012), urgency-based and functionally referential alarm

calls (Manser 2001; Manser et al. 2001; Manser et al. 2002). However, less is known about the alarm-call systems of other mongoose species.

Dwarf mongooses are social mongooses with a despotic social structure (Rasa 1987; Keane et al. 1994) comparable to that of meerkats (Clutton-Brock et al. 2001). They live in groups of up to 30 individuals (Rasa 1977) with reproduction generally limited to the dominant pair; related and unrelated subordinate group members cooperatively help to rear the young (Keane et al. 1994). Dwarf mongooses live in woodlands or wooded savannas (Sharpe et al. 2015) where visibility is potentially reduced, making predator detection more difficult, whilst their small size makes them vulnerable to a wide range of predators, both aerial and terrestrial (Rasa 1986; Kern and Radford 2014). A past study on dwarf mongooses suggests that they may have an even more sophisticated alarm-call system than meerkats, with alarm calls encoding not only predator species and urgency level, but also specifically distance and elevation (Beynon and Rasa 1989). However, this study was carried out on a single group of captive mongooses and the information receivers extract from these calls remains to be experimentally tested. We followed up these preliminary observations and investigated how dwarf mongooses both use and perceive warning signals, with the aim of providing a detailed description of their alarm-call system in the wild and providing further data for cross-species comparisons.

First, using a combination of behavioural observations, predator presentations and acoustic analysis, we document the different alarm-call types produced by dwarf mongooses in the wild. In accordance with Beynon and Rasa's (1989) findings in a single group of captive mongooses, we predicted that callers would produce structurally distinct alarm calls to aerial and terrestrial predators. Second, we carried out playback experiments, testing responses to the call types that the observational data and predator presentations identified as most likely to be aerial and terrestrial alarm calls. In line with behavioural responses observed in meerkats (Manser et al. 2001), we expected receivers to run for shelter and look at the sky in response to an aerial alarm, and to gather together and scan the area horizontally when hearing a terrestrial alarm call.

METHODS

Study Site and Species

The study was carried out on Sorabi Rock Lodge Reserve, a 4 km^2 private game reserve in Limpopo Province, South Africa (24°11'S, 30°46'E). For more detailed information about this study site, see Kern and Radford (2013). All data were collected between November 2014 and June 2015 and in January–February 2016 from adult (>1 year of age) wild dwarf mongooses belonging to seven different groups (mean group size: 11; range: 6–15). All mongooses were habituated to close observation on foot (<5 m) and individually identifiable by distinctive hair-dye marks (Wella UK Ltd., UK) or scars.

Acoustic Recording Methods

All acoustic recordings were saved onto a PNY SD card (PNY, Parssipany, NJ, U.S.A.) using a Marantz PMD661 MKII solid-state recorder (D&M Holding, Inc., Kanagawa, Japan; sampling rate 44.1; 24 bit accuracy) attached to a Sennheiser ME66/K6 directional microphone (Sennheiser Electronic Corp., Old Lyme, CT, U.S.A.) with a windshield (Rycote Microphone Windshields, Stroud, Gloucestershire, U.K.). Whenever an alarm call was produced, it was marked on the audio file. Where possible, the external stimulus that elicited the alarm call, the mongooses' response, and the caller's identity were spoken into a microphone (TG V30d s, Beyerdynamic, Heilbronn, Germany) linked to a second channel. When considering the call types produced in relation to stimulus type, we took into account all alarm calls recorded. However, when assessing the alarm-call responses, we only considered the reaction to the first call in a bout, with a bout being defined as a series of calls separated by <10 s from each other. The reaction to the first call in a bout was nearly always the strongest response and, furthermore, any reaction to the subsequent calls seemed to be influenced by the reaction to the first call (Collier pers. obs.).

Dwarf mongoose groups were followed for approximately three hours in the morning after they left the sleeping burrow and another 2–3 hours in the evening until they returned to a sleeping burrow for the night. All vocalisations were recorded ad libitum (Altmann 1974). To obtain additional recordings of alarms calls, especially those given in response to terrestrial predators for which we observed no natural encounters, simulated predator presentations were conducted. Given that preliminary experiments showed dwarf mongooses did not respond to taxidermy models of animals (Collier et al. unpub. data), we used a live domestic dog (*Canis lupus*

familiaris). The dog, on a lead, was walked slowly towards the mongoose group, stopped between 15 and 30 m away from the group once the mongooses reacted, and then walked slowly away until it was out of sight again around 50 m from the group. To simulate aerial predator encounters, we used a large helium balloon (88 x 22 x 10 cm) in the shape of the number 6 or 8. The experimenter holding the balloon remained hidden 20–40 m from the group behind bushes or small trees, and released the balloon until it was visible to the mongooses above the vegetation. We recorded all alarm calls produced in response to these presentations (using the equipment described above) and filmed their responses on a Canon Legria HF R506 handheld camcorder (Cannon Inc., Tokyo, Japan).

Acoustic Analysis

Spectrograms of the alarm calls were generated using Praat version 5.3.85 (www.praat.org). We first divided the alarm calls into different classes by ear and visual inspection of the spectrograms, as in Candiotti et al. (2012). We excluded recruitment calls, given when the mongooses encounter a snake and that provoke a mobbing response, as they are described elsewhere (Kern and Radford in revision). We labelled each alarm-call type with a number reflecting the order in which the call types were identified. Due to the rare occurrence of some of the dwarf mongoose alarm calls, we focused our acoustic analyses on the five most commonly produced types (see Results). We selected calls with a good signal-to-noise ratio and, using the bioacoustics software Luscinia (Lachlan, 2007), we extracted a number of temporal and spectral parameters: call length (ms); overall and mean peak frequency (Hz); maximum and minimum peak frequency (Hz); mean, maximum and minimum fundamental frequency (Hz); mean change in peak and fundamental frequency expressed on an arctan scale (0 means decreasing infinitely quickly, 1 increasing infinitely quickly and 0.5 indicates no change); mean Wiener entropy, mean frequency bandwidth (Hz); number of elements; and within-syllable gap (ms) (table 1).

Table 1: Description of the acoustic parameters measured for the alarm calls. The parameters in bold were entered into the permutated discriminant function analysis (pDFA).

Acoustic parameter	Description
Call length	Time elapsed between the beginning and the end of the call.
Overall peak frequency	Peak frequency is the frequency of maximum amplitude within one spectrum of the spectrogram. Overall peak frequency is the frequency of maximum amplitude within the call.
Mean peak frequency	Mean of all peak frequencies within the call.
Maximum peak frequency	Peak frequency of highest peak frequency within the call.
Minimum peak frequency	Peak frequency of the lowest peak frequency within the call.
Mean fundamental frequency	Average fundamental frequency across the whole call. Fundamental frequency is the lowest frequency of a periodic waveform.
Maximum fundamental frequency	Fundamental frequency of highest frequency within the call.
Minimum fundamental frequency	Fundamental frequency of lowest frequency within the call.
Mean change in peak frequency	Mean change in peak frequency over time.
Mean change in fundamental frequency	Mean change in fundamental frequency over time.
Mean Wiener entropy	A measure of noisiness: Ratio of the geometric mean to the arithmetic mean of the power spectrum.
Mean frequency bandwidth	Frequency difference between the first and final maximum intensity in the signal.
Number of elements	Number of continuous traces on the spectrogram that compose the call.
Within-syllable gap	Total duration of silence between the elements of a call.

Playback Stimuli and Experimental Procedure

To test whether dwarf mongooses responded differently to alarm calls given to aerial and terrestrial predators (see Results), we carried out playback experiments using the call types that most frequently accompanied aerial and terrestrial encounters respectively (alarm-call types 1 and 4, see figure 1). To generate the playback stimuli, we only used alarm calls with a good signal-to-noise ratio, resulting in 15 exemplars of alarm-call type 1 and 12 of alarm-call type 4. We only used alarm calls recorded from a different group to that of the subject to ensure that the latter did not hear its own calls during the experiment. The amplitude of the playback was set by ear to be equivalent to that of a naturally produced alarm call.

Each alarm-call type was played back to 17 focal adult mongooses from seven different groups. For each stimulus, one individual out of the 17 was opportunistically tested twice, once in each field season, giving a total of 18 playbacks for each alarm-call type. All alarm-call exemplars were used once, with several randomly selected exemplars used a second time for the remaining trials. Alarm calls were played back from a height of around 1 m, simulating an alarm call from a mongoose acting as a sentinel; an individual adopting a raised position to scan for danger (Kern and Radford 2013). Playbacks were started when the test subject was foraging in the open and its response was filmed with a handheld camcorder (as above). In line with previous work, we scored the response strength of the focal mongoose reaction as: 1=no reaction (when there was no visible change in behaviour); 2=vigilant (when the mongoose paused foraging and scanned the area horizontally); 3=moved (when the mongoose took a few steps forwards but stopped short of cover); or 4=ran for cover (when the mongoose moved quickly to the nearest bush or rocks) (Blumstein and Armitage 1997a; Fischer and Hammerschmidt 2001; Suzuki 2015). We also measured the focal individual's latency to relax; that is, time to resume foraging or start grooming, in seconds. Additionally, we noted other behaviours potentially associated with predator encounters that occurred within 1 min of the playback. These included looking at the sky, which may allow the mongooses to detect aerial threats, and becoming a sentinel, which may improve the detection of any kind of predator. Playbacks were only performed if no alarm calls (conspecific or heterospecific) had been heard for at least 10 min, and no playbacks were carried out if the mongooses were showing signs of alarm or arousal from previous events such as predator encounters or intergroup interactions. To minimise the likelihood of habituation, playbacks were separated by at least 1 h. We carried out a maximum of three playbacks a day to a given group, over one or two sessions (morning and afternoon), but on one occasion we conducted four playbacks in a day over two sessions. This was well

below the average of 20 alarm calls recorded per hour during observations (Collier unpub. data).

Statistical Analysis

a) Acoustic analysis

We calculated the variance inflation factors (VIF) of the measured acoustic parameters to determine which were collinear. We removed the parameter with the highest VIF and repeated the procedure until all the remaining acoustic parameters had a VIF inferior to 6 and hence should be free from multi-collinearity (Belsley et al. 2005). We then entered the remaining parameters into a discriminant function analysis (DFA). However, as we had repeated measures, with multiple recordings from the same group, which can lead to inflated significance in conventional DFAs (Mundry and Sommer 2007), we conducted a crossed permutated discriminant function analysis (pDFA) using a function provided by R. Mundry (Cäsar, Byrne, Young, et al. 2012; Clay et al. 2015). Permutated DFAs allow for repeated measures linked to multiple recordings from the same individual or group and avoid inflation or over-estimation of p-values. All statistics were carried out using R version 3.2.1 (R Core Team 2015) with the packages usdm (Naimi 2013) and MASS (Venables and Ripley 2002).

b) Playbacks

To investigate the strength of response in relation to stimuli type, we carried out Cumulative Link Mixed Models (CLMMs) using the ordinal package in R (Christensen 2015). For latencies to relax, we performed Linear Mixed Models (LMMs), using R package lme4 (Bates et al. 2015). Diagnostic tests indicated there were no violations of the assumptions of linearity, homoscedasticity and normality of the residuals. Finally, given the binomial nature of the looking behaviour (looked up or not) and sentinel behaviour (sentinel or not) we used Generalized Linear Mixed Models (GLMMs) with a binomial family and a logit link function to test whether these variables differed across playback types. As some individual mongooses were used as subjects more than once and multiple individuals from the same group were tested, we nested individual within group and fitted this as random effect whilst the stimulus type (alarm-call type 1 or 4) was fitted as a fixed effect. We calculated p-values using likelihood

ratio tests that compare full models, including all the explanatory variables, to reduced models that include the same explanatory variables with the exception of the variable of interest.

Ethical Note

Our work was carried out under permission from the Limpopo Department of Economic Development, Environment and Tourism (permit number: 001-CPM403-00013) and the Ethical Committee of Pretoria University, South Africa (permit number: EC049-16).

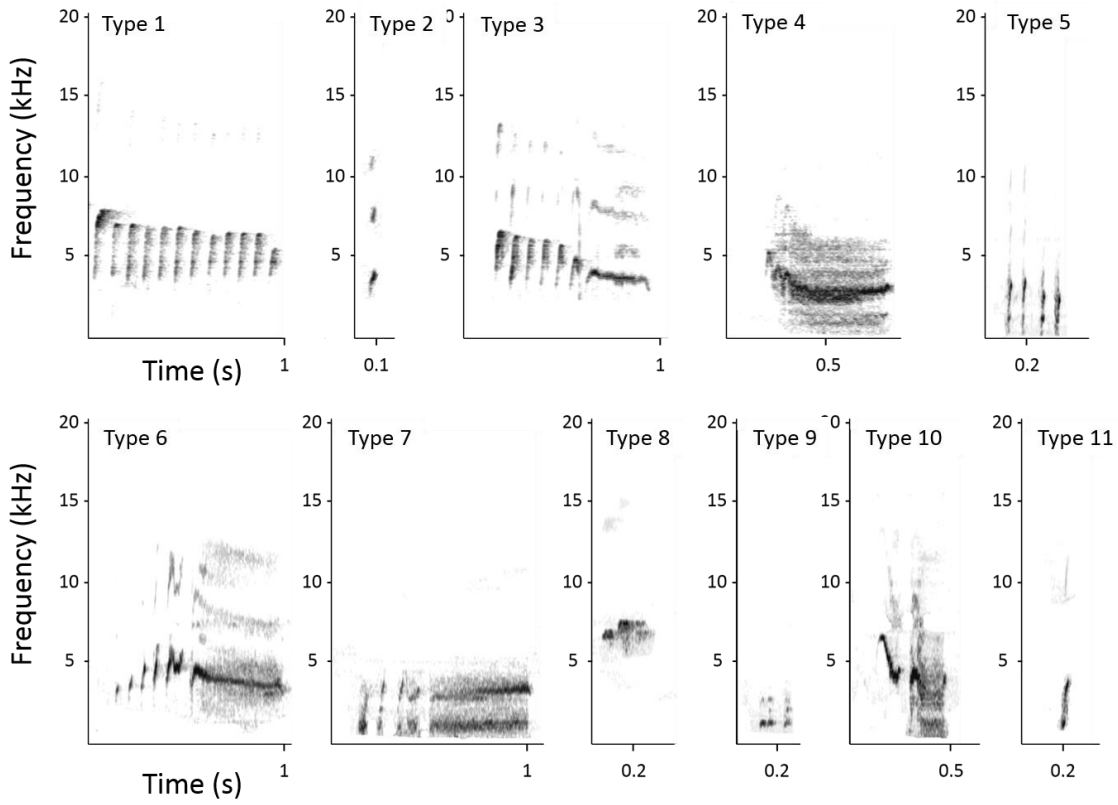

Figure 1: Spectrograms of the alarm calls present in the dwarf mongoose repertoire.

RESULTS

Dwarf Mongoose Alarm-Call Repertoire

We obtained over 150 h of recordings from seven mongoose groups (range: 12–43 h per group). From these recordings, we collected 900 alarm calls from 402 bouts that were given to an identifiable external stimulus other than the observer and 588 alarm calls from 349 bouts that were given to the observer. The remaining 1196 alarm calls, recorded from 463 bouts, were

given to unidentified stimuli and so are not discussed further here. Visual inspection of the spectrograms suggested these alarm calls could be divided into 11 different types, some of which seemed to resemble combinations of two other alarm calls (figure 1). Five of the alarm-call types were more commonly produced, with the remaining six alarm-call types each recorded 41 times or less over the study period. Statistical analysis confirmed that the five most-produced alarm-call types could also be distinguished by their acoustic parameters alone, with significantly more calls being correctly cross-classified in the respective groups than expected by chance (pDFA, percentage correctly classified = 89%, p=0.001) (figure 2).

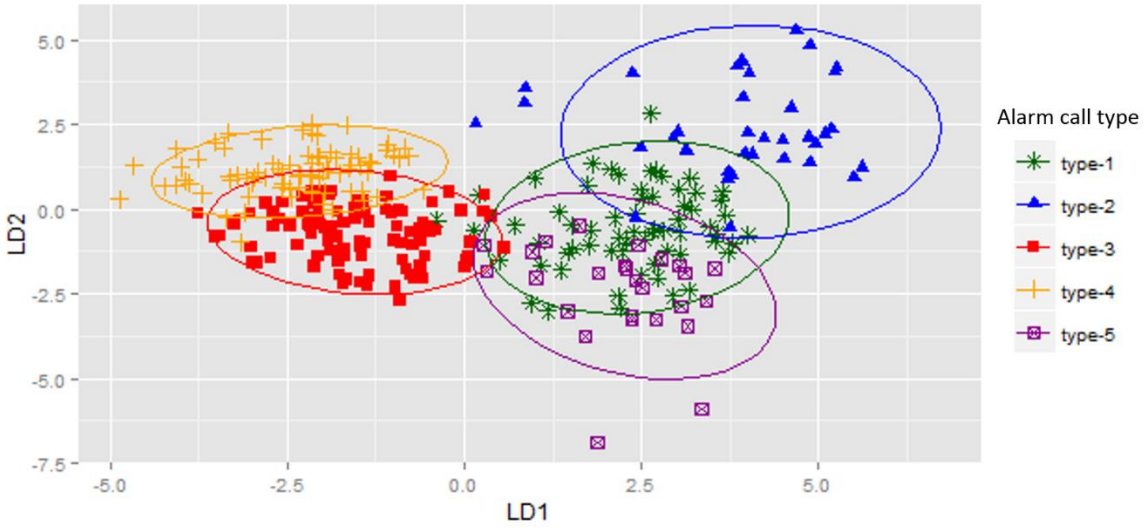

Figure 2: Output of the discriminant function analysis of the acoustic parameters of the 5 most common alarm calls produced by dwarf mongooses. This figure shows the distribution of discriminant scores along the two principal discriminant functions. LD: linear discriminant function.

Alarm-Call Production

During natural observations, dwarf mongooses gave alarm calls to various external stimuli that included physically present animals of both predatory and non-predatory species, and, presumably, scents which can be secondary cues of predators or competing mongoose groups (Christensen et al. 2016; Morris-Drake et al. in press). These stimuli could be divided into 11 different categories (table 2). The same alarm-call type could be given to several types of stimuli (table 3), however there were differences in the production of alarm-call types in response to the diverse stimuli. For example, the main alarm calls given to aerial stimuli were

"type 1" alarm calls which represented 55% of calls given to this stimulus category and constituting 73% of all type 1 alarm calls produced. "Type 3" alarm calls made up 25% of calls given to aerial stimuli, constituting 78% of all type 3 alarm calls. Whilst 26% of "type 2" alarms were likewise given to aerial stimuli, this constituted only 9% of calls given to this stimulus. The principal alarm call given to the observer was alarm call "type 4" (34% of calls given to this stimulus), representing 44% of all type 4 calls produced. Type 3 alarm calls also formed a large portion of the calls given to the observer (25%), followed by type 2 (20%) and type 1 (12%). The principal alarm call given to terrestrial scents was type 4 (93%), constituting 52% of type 4 alarm calls emitted.

Table 2: Different categories of external stimuli to which dwarf mongooses produced alarm calls.

Category	Description
Aerial stimuli	Includes flying birds of prey, flying non-predatory birds and aircraft such as planes or helicopters
Antelope	Includes impala and duiker
Banded mongoose	Banded mongoose
Dog	Dog during predator presentations
Heterospecific alarm	Alarm calls given by non-predatory birds, tree squirrels and impala
Moving branches	Branches moving in the wind
Observer	Human researcher or any part of her equipment (e.g. microphone)
Perched bird	Predatory and non-predatory birds perched in a tree
Primates	Includes vervet monkeys and baboons, both on the ground or in trees
Small terrestrial	Includes hares and tree squirrels moving on the ground
Scent	Specific section of rocks or trees when no other potential stimulus was visible, possible dwarf mongoose or predator latrines

Although the mongooses produced eight different types of alarm call when presented with the dog, 69% of them were type 4 alarm calls and 17% of them were type 3 alarm calls. The other call types were each recorded 13 times or less. The dwarf mongooses produced seven different alarm-call types in response to the helium balloon presentation; 45% of them were type 3, 41% type 1 and 10% type 2 alarm calls. All the other alarm-call types were produced seven times or less (table 4).

Table 3: The number of alarm calls of each type produced in response to each stimulus category. Type 8 is not represented in this table as it was only produced in response to predator presentations. A call bout is defined as a series of alarm calls separated by an interval of less than 10 seconds.

	type-01	type-02	type-03	type-04	type-05	type-06	type-07	type-09	type-10	type-11	**Total**	**N call bouts**
aerial	272	44	124	10	31	3	3	3	0	4	**494**	**150**
antelope	3	0	1	2	0	2	2	1	0	1	**12**	**6**
banded mongoose	2	0	27	1	10	2	0	3	0	0	**45**	**5**
heterospecific alarm	17	6	1	0	18	0	0	4	0	1	**47**	**34**
observer	73	116	145	199	20	33	0	0	2	0	**588**	**419**
Moving branches	0	1	0	0	0	0	0	0	0	0	**1**	**1**
perched bird	5	1	3	1	1	0	0	0	0	0	**11**	**5**
primate	1	0	2	6	13	0	0	8	0	0	**30**	**10**
scent	0	0	1	235	1	0	2	0	13	0	**252**	**188**
small terrestrial	1	1	0	0	3	0	0	2	0	0	**7**	**2**
Total	**374**	**169**	**304**	**454**	**97**	**41**	**7**	**21**	**15**	**6**	**1488**	**820**

Responses to Alarm Calls

Where a response was reported in reaction to a naturally produced alarm call, mongooses were already under cover in 19% of the cases for which they heard a type 1 alarm call. In the remaining cases, the mongooses either ran for cover 47% or went vigilant 39% of the time. The rest of the time (14%), the mongooses showed no reaction or moved slightly without reaching cover. In 77% of the cases after hearing a type 2 alarm call, the mongooses ran for cover. When hearing a type 3 alarm, subjects were already under cover in 15% of the cases and went vigilant

in 94% of the remaining cases. Mongooses went vigilant 92% of the time after hearing a type 4 alarm-call. Finally, they were either vigilant 65%, ran for cover 20% or moved 10% of the time after hearing a type 5 alarm call (table 5).

Playback experiments verified that stimulus type had a significant effect on response strength (CLMM: χ^2=7.01, N=36, df=1, p=0.008). Specifically, subjects reacted more strongly in response to a type 1 than a type 4 alarm call (figure 3). In response to a type 1 alarm call, most mongooses ran for cover (12/18), whereas in response to a type 4 alarm-call, most of them went vigilant, looking out horizontally (12/18). Mongooses only looked at the sky in response to a type 1 and never in response to a type 4 alarm call (respectively 5/18 and 0/18 times; GLMM: χ^2=7.39, N=36, df=1, p=0.007). However, they showed no significant difference in latency to relax (LMM: χ^2=1.05, N=36, df=1, p=0.31) or likelihood to become a sentinel (GLMM: χ^2=0.21, N=36, df=1, p=0.65).

Table 4: The number of alarm calls of each type produced in response to each type of predator presentation.

	type-01	type-02	type-03	type-04	type-05	type-06	type-07	type-08	type-09	type-11	**Total**
dog	2	3	48	194	13	6	1	0	9	4	**280**
helium balloon	197	49	216	0	7	1	6	2	0	0	**478**

Table 5: Dwarf mongoose responses to the first alarm call in a bout in relation to its type when hearing a naturally produced alarm call.

	type-01	type-02	type-03	type-04	type-05	type-06	type-07	type-09	type-10	type-11	**Total**
under cover	12	0	3	0	0	0	0	0	0	0	**15**
latrine	0	0	0	1	0	0	0	0	0	0	**1**
moved	5	2	0	1	2	0	0	1	0	1	**12**
no reaction	2	0	0	10	1	0	0	0	0	0	**13**
ran to cover	24	10	1	0	4	0	3	0	0	1	**43**
sniffing	0	0	0	2	0	0	0	0	1	0	**3**
vigilant	20	1	16	167	13	1	0	3	0	2	**223**
Total	**63**	**13**	**20**	**181**	**20**	**1**	**3**	**4**	**1**	**4**	**310**

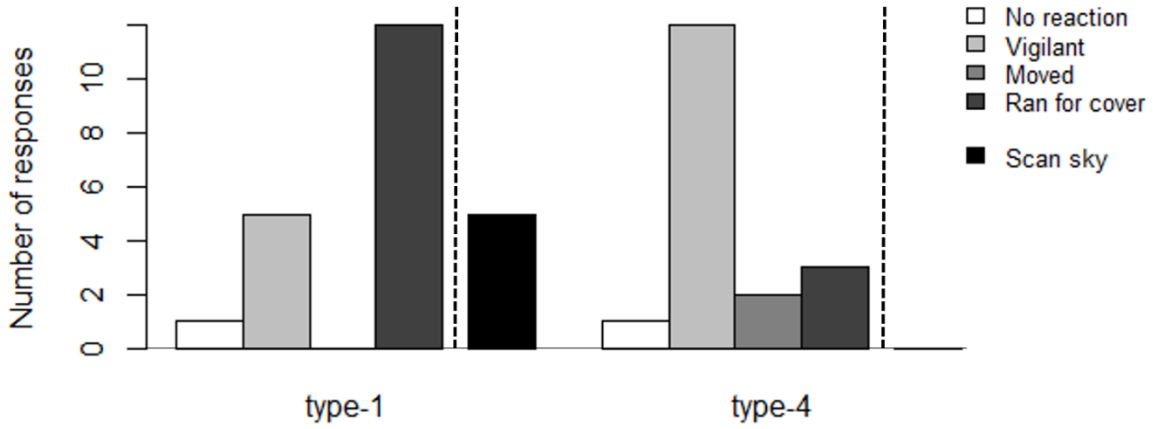

Figure 3: Dwarf mongooses' main mutually exclusive responses to the playbacks of type 1 and type 4 alarm calls and, to the right of the dashed line, an additional, non mutually-exclusive, behaviour, scanning the sky. $N_{(type\ 1)}$=18, $N_{(type\ 4)}$=18.

DISCUSSION

Dwarf Mongoose Alarm Calls

Overall, we found that adult dwarf mongooses produced 11 distinct types of alarm call, of which only five were commonly produced. This is less than the 14 alarm-call types that dwarf mongooses were previously reported to produce (Rasa 1984; Manser et al. 2014). However, in the current study, we did not include recruitment and mobbing calls, which may explain the observed variation in alarm-call number. The alarm calls we recorded were given to 11 different types of stimuli that included both potential predators, such as raptors and dogs, and, contrary to previous studies (Rasa 1983), non-predators including antelope, small terrestrial animals and non-predatory birds, especially if they appeared suddenly. Thus, the dwarf mongooses observed in this study sometimes produced alarm calls in response to non-predatory animals or even moving objects (planes, helium balloons). This was not reported for mongooses in the Taru desert, Kenya, that were only ever recorded producing alarm calls in response to animals known to prey on dwarf mongooses (Rasa 1983). This difference is most likely due to differing observation methods as our recordings were carried out from within the group rather than at a distance, increasing our chances of detecting the majority of alarm calls.

Risk Related Alarm Calls

Based on the responses they elicited and the multiple stimuli the different alarm calls were given to, alarm-call types 2, 3 and 5 appeared to be risk related. Type 2 alarm calls seemed to provoke a stronger response than any other alarm call, resulting in subjects running for cover 77% of the time, suggesting that these alarm calls may be high risk calls. These calls were mostly given to the observer. This could be linked to the often close proximity of observers to the group and the possibility of them startling mongooses emerging from the undergrowth. Type 2 alarm calls were also often given to aerial stimuli, however they represented a very small portion of the calls given in such events. This result may be due to aerial predators being more likely to represent a higher level of threat than other stimulus types due to their speed of approach (Blumstein and Armitage 1997a). Alarm-call types 3 and 5 were produced non-specifically in response to a variety of stimuli. Type 3 alarm calls were produced in relatively high proportions for both the helium balloon and dog presentations and in response to the observer, as well as being the main alarm call given to banded mongooses. Type 5 alarm calls were emitted in response to aerial stimuli, observers, heterospecific alarm calls, primates and banded mongooses. The main natural response to both of these alarm calls is for the subjects to become vigilant, indicating that they may be general, lower risk alarm calls.

Predator-Specific Alarm Calls

Alarm-call types 1 and 4 appeared to be associated with specific types of threat. The majority of these calls recorded during natural encounters with predators were given respectively to aerial stimuli and to scents. Dwarf mongooses can react to scents or secondary cues left by predators (Morris-Drake et al. in press) or conspecifics from another group (Christensen et al. 2016), both of which can represent a threat. Hence, we considered scents to be indirect secondary cues of terrestrial threats. Additionally, predator presentations showed that alarm-call type 1 is one of the principal calls given to helium balloons (in the air) and alarm-call type 4 is the primary call given to terrestrial predators. Furthermore, test subjects reacted differently to the playbacks of these two call types. Subjects were more likely to react strongly to a type 1 alarm, running for cover, and looking up at the sky after hearing this call type. These responses are consistent with, for example, avoiding an imminent attack coming from above. Subjects did not react as strongly to type 4 alarm calls. Though, contrary to our prediction, receivers did not gather together when hearing a type 4 alarm call, their responses corresponded with the

contexts of production, with subjects primarily becoming vigilant, looking out horizontally. Terrestrial predators can attack from any direction on the ground, therefore scanning the environment to detect the location of the danger before reacting could potentially improve the receiver's chances of survival. Furthermore, as type 4 alarm calls are given to both terrestrial predators and secondary cues, receivers may rely on visual cues to distinguish the two. Since alarm-call types 1 and 4 are given to specific predator classes and they elicit adaptive responses from receivers even in the absence of external stimuli, we argue they fit the definition of functionally referential alarm calls (Macedonia and Evans 1993). Previous work has demonstrated that predator-specific alarm calls can also carry information about perceived urgency (Manser et al. 2001; Manser et al. 2002). Further research taking into account, for example, predator distance, would allow us to determine if this is also the case for dwarf mongoose aerial and terrestrial alarm calls.

Whilst both type 1 and type 4 alarm calls fulfil the requirements set out to determine functionally referential calls (Macedonia and Evans 1993), dwarf mongoose aerial alarm calls seem to show more production specificity, being given to a narrower category of stimuli than terrestrial alarm calls. Aerial alarm calls are only given to visible aerial threats, whereas terrestrial alarm calls are given to both visible terrestrial predators and secondary cues, namely scents. A similar pattern is seen in several primate species, with the terrestrial alarm call being less specific than the aerial alarm, to the point where it is not considered referential (red-fronted lemurs, *Eulemur fulvus rufus* and Verreaux sifakas, *Propithecus verreauxi*: Fichtel and Kappeler 2002; tufted capuchins, *Cebus apella nigritus*: Wheeler 2010). By contrast, Gunnison's prairie dogs distinguish between several different types of terrestrial predators, producing different alarm calls in response to coyotes (*Canis latrans*), domestic dogs and humans (*Homo sapiens*) (Kiriazis and Slobodchikoff 2006).

Production specificity of a functionally referential alarm call may be linked to the response specificity of the receiver, with the categories to which alarm calls are given being defined by the categories to which receivers show distinct responses. For example, dwarf mongooses show the same response, specifically vigilance, whether an alarm call is elicited by a potential terrestrial predator (e.g. dog) or by a secondary cue. On the other hand, prairie dogs show different responses to various terrestrial predators (Kiriazis and Slobodchikoff 2006), and meerkats and banded mongoose emit distinct calls to predators and their secondary cues (Manser 2001; Furrer & Manser 2009a), causing different responses in the receivers (Manser et al. 2001; Furrer & Manser 2009a). Alternatively, production specificity of functionally

referential alarm calls may be a function of urgency to respond to a certain category of predators. Producing an alarm to a narrower predator category could allow the receiver to react appropriately and rapidly to the situation, which may be crucial to its survival if this predator presents an immediate, high threat. However, if an immediate response is not critical to survival, a less specific call given to a wider category of predators may be sufficient as the receiver would have time to integrate contextual cues before responding appropriately (Manser 2009; Wheeler and Fischer 2012; Price et al. 2015). This would support the suggestion that attributing meaning to a less specific alarm call is more cognitively demanding on the receiver's part than for a more specific call as individuals would need to take into account not only the call but also external contextual cues (Wheeler and Fischer 2012).

Dwarf mongooses produced both terrestrial (type 4) and aerial (type 1) alarm calls in response to human observers. As the majority of these calls were terrestrial alarm calls, this would potentially suggest that dwarf mongooses principally classified observers as terrestrial. However, as noted above, subjects also produced aerial alarm calls in response to researchers, suggesting that the mongooses occasionally perceived observers as aerial. Such classification could be the result of the close proximity of human observers to the group and hence presenting a greater saliency in the vertical rather than the horizontal plane. Furthermore, observers often carried microphones attached to a pole that may be detected independently of the researcher if the latter is hidden by vegetation, thus appearing to be aerial. Additionally, a large number of type 3 alarm calls were produced in response to the observer. As type 3 is a general alarm call (Collier et al. in prep.), as opposed to a predator-specific alarm, this further points towards the observer as a potentially ambiguous stimulus.

Comparison with other Mongoose Species

The dwarf mongoose alarm-call system is similar in size and content to the repertoire of meerkats that also includes both functionally referential and urgency related alarm calls (Manser 2001), despite differences in habitat between the two species. However, the dwarf mongoose's alarm-call repertoire is larger than those documented in other closely-related mongoose species exposed to similar predators, including social species, banded mongooses (four alarm calls), and more solitary species, yellow mongooses (*Cynictis penicillata*) and slender mongooses (respectively four and two alarm calls) (Manser et al. 2014). Differences in social system could explain the discrepancy in repertoire size between these species. Indeed it

has been hypothesised that more socially complex species, often measured by group size, will also have a more complex vocal system, mostly quantified via repertoire size (Freeberg et al. 2012), as is the case in taxa such as primates (McComb and Semple 2005) and whales (May-Collado et al. 2007). However, in other taxa, including mongooses and mole-rats, repertoire sizes does not seem to be dependent on group size, but possibly on other social factors such as social structure (Manser et al. 2014). This is illustrated by the banded mongooses, that can live in groups of up to 70 individuals (Cant 1999) but produce fewer alarm calls than dwarf mongooses that are rarely found in groups of more than 30 individuals (Rasa 1977). Given these two species also share a habitat, being partially sympatric (Sharpe et al. 2015; Hoffman 2008), and similar types of predators, including raptors and terrestrial predators (Rood 1983; Rasa 1986), these two factors are unlikely to influence the difference in alarm-call repertoire size. Instead discrepancy in alarm-call repertoire size may be related to the fact that banded mongooses seem to produce urgency related but no predator-specific alarm calls (Jansen 2013). What remains unclear is why banded mongooses do not emit functionally referential alarm calls despite their similarities in social structure and predator risks with both meerkats and dwarf mongooses. Potentially banded mongooses, unlike dwarf mongooses and meerkats, may use the same escape strategy for all predator types, perhaps because they are able to use nearby vegetation as immediate shelter and their larger size and larger groups may make them less vulnerable to predation, thus making urgency more relevant than predator type. Therefore, for mongoose species, habitat does not seem to play a role in favouring the emergence of functionally referential alarm calls, with species from both semi-arid areas and woodlands producing such alarm calls. Sociality on the other hand may have some impact as, to our knowledge, functionally referential alarm calls are only produced by the more social mongoose species. However, sociality alone does not seem to explain the presence of a functionally referential alarm-call system. Thus, it seems that functionally referential alarm-call systems may be more likely to emerge in species presenting both differing escape strategies and a complex social structure involving the need to coordinate cohesive group movement.

Conclusion

In conclusion, wild dwarf mongooses have a large repertoire of alarm calls, comparable in size and function to that of the closely-related meerkats. Dwarf mongooses produce both urgency related and functionally referential alarm calls. However, contrary to previous work on a single

group of captive mongooses by Beynon and Rasa (1989), the mongooses in this study did not seem to produce species-specific alarm calls for raptors. Unlike other mongoose species, they seem to use the same alarm call for both physically present terrestrial predators and secondary cues of their presence. Further work would be needed to investigate the function of the rarer alarm calls and to determine if other forms of information, such as distance and elevation of the predator, are also transmitted in wild mongoose alarm calls.

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REFERENCES

Ackers SH, Slobodchikoff CN. 1999. Communication of stimulus size and shape in alarm calls of Gunnison's prairie dogs, *Cynomys gunnisoni*. Ethology 105:149–162.

Altmann J. 1974. Observational study of behavior: sampling methods. Behaviour 49:227–266.

Bates D, Meachler M, Bolker BM, Walker S. 2015. lme4: Linear mixed-effects models using Eigen and S4.

Belsley DA, Kuh E, Welsch RE. 2005. Regression diagnostics: Identifying influential data and sources of collinearity. New York, NY, USA: John Wiley & Sons.

Beynon P, Rasa OAE. 1989. Do dwarf mongooses have a language?: Warning vocalisations transmit complex information. South Afr. J. Sci. 85:447–450.

Blumstein DT. 2007. The evolution, function, and meaning of marmot alarm communication. Adv. Study Behav. 37:371–401.

Blumstein DT, Armitage KB. 1997a. Alarm calling in yellow-bellied marmots: I. The meaning of situationally variable alarm calls. Anim. Behav. 53:143–171.

Blumstein DT, Armitage KB. 1997b. Does sociality drive the evolution of communicative complexity? A comparative test with ground-dwelling sciurid alarm calls. Am. Nat. 150:179–200.

Blumstein DT, Arnold W. 1995. Situational specificity in Alpine-marmot alarm communication. Ethology 100:1–13.

Candiotti A, Zuberbühler K, Lemasson A. 2012. Context-related call combinations in female Diana monkeys. Anim. Cogn. 15:327–339.

Cant MA. 1999. Communal breeding in banded mongooses and the theory of reproductive skew. University of Cambridge.

Cäsar C, Byrne RW, Hoppitt W, Young RJ, Zuberbühler K. 2012. Evidence for semantic communication in titi monkey alarm calls. Anim. Behav. 84:405–411.

Cäsar C, Byrne RW, Young RJ, Zuberbühler K. 2012. The alarm call system of wild black-fronted titi monkeys, *Callicebus nigrifrons*. Behav. Ecol. Sociobiol. 66:653–667.

Christensen C, Kern JM, Bennitt E, Radford AN. 2016. Rival group scent induces changes in dwarf mongoose immediate behavior and subsequent movement. Behav. Ecol.:arw092.

Christensen RHB. 2015. Ordinal - Regression Models for Ordinal Data.

Clay Z, Archbold J, Zuberbühler K. 2015. Functional flexibility in wild bonobo vocal behaviour. PeerJ 3:e1124.

Clutton-Brock TH, Brotherton PNM, Russell AF, O'riain MJ, Gaynor D, Kansky R, Griffin A, Manser MB, Sharpe LL, McIlrath GM, et al. 2001. Cooperation, control, and concession in meerkat groups. Science 291:478–481.

Collier K, Radford AN, Stoll S, Manser MB, Bickel B, Townsend SW. in prep. Meaningful call combinations in the alarm call system of dwarf mongooses (*Helogale parvula*): evidence for disjunction?

Fichtel C, Kappeler PM. 2002. Anti-predator behavior of group-living Malagasy primates: mixed evidence for a referential alarm call system. Behav. Ecol. Sociobiol. 51:262–275.

Fischer J, Hammerschmidt K. 2001. Functional referents and acoustic similarity revisited: The case of Barbary macaque alarm calls. Anim. Cogn. 4:29–35.

Freeberg TM, Dunbar RIM, Ord TJ. 2012. Social complexity as a proximate and ultimate factor in communicative complexity. Philos. Trans. R. Soc. Lond. B Biol. Sci. 367:1785–1801.

Furrer RD, Manser MB. 2009a. Banded mongoose recruitment calls convey information about risk and not stimulus type. Anim. Behav. 78:195–201.

Furrer RD, Manser MB. 2009b. The evolution of urgency-based and functionally referential alarm calls in ground-dwelling species. Am. Nat. 173:400–410.

Griesser M. 2008. Referential calls signal predator behavior in a group-living bird species. Curr. Biol. 18:69–73.

Hoffman M. 2008. *Mungos mungo*. IUCN red list of threatened species.

Jansen DAWAM. 2013. Vocal communication in the banded mongoose [PhD]. [Zurich, Switzerland]: University of Zurich.

Keane B, Waser PM, Creel SR, Creel NM, Elliott LF, Minchella DJ. 1994. Subordinate reproduction in dwarf mongooses. Anim. Behav. 47:65–75.

Kern JM, Radford AN. in revision. Social-bond strength influences vocally-mediated recruitment to mobbing. Biol. Lett.

Kern JM, Radford AN. 2013. Call of duty? Variation in use of the watchman's song by sentinel dwarf mongooses, *Helogale parvula*. Anim. Behav. 85:967–975.

Kern JM, Radford AN. 2014. Sentinel dwarf mongooses, *Helogale parvula*, exhibit flexible decision making in relation to predation risk. Anim. Behav. 98:185–192.

Kiriazis J, Slobodchikoff CN. 2006. Perceptual specificity in the alarm calls of Gunnison's prairie dogs. Behav. Processes 73:29–35.

Lachlan, R.F. (2007). Luscinia: a bioacoustics analysis computer program.

Leavesley AJ, Magrath RD. 2005. Communicating about danger: urgency alarm calling in a bird. Anim. Behav. 70:365–373.

Macedonia JM. 1990. What is communicated in the antipredator calls of lemurs: evidence from playback experiments with ringtailed and ruffed lemurs. Ethology 86:177–190.

Macedonia JM, Evans CS. 1993. Essay on contemporary issues in ethology: Variation among mammalian alarm call systems and the problem of meaning in animal signals. Ethology 93:177–197.

Manser MB. 2001. The acoustic structure of suricates' alarm calls varies with predator type and the level of response urgency. Proc. R. Soc. B Biol. Sci. 268:2315–2324.

Manser MB. 2009. What Do Functionally Referential Alarm Calls Refer To? In: Cognitive ecology II. Chicago, IL, USA: University of Chicago Press. p. 229–246.

Manser MB, Bell MB, Fletcher LB. 2001. The information that receivers extract from alarm calls in suricates. Proc. R. Soc. B Biol. Sci. 268:2485–2491.

Manser MB, Jansen DAWAM, Graw B, Hollén LI, Bousquet CAH, Furrer RD, le Roux A. 2014. Vocal complexity in meerkats and other mongoose species. In: Advances in the Study of Behavior. Vol. 46. Elsevier. p. 281–310.

Manser MB, Seyfarth RM, Cheney DL. 2002. Suricate alarm calls signal predator class and urgency. Trends Cogn. Sci. 6:55–57.

Marler P. 1967. Animal communication signals. Science 157:769–774.

May-Collado LJ, Agnarsson I, Wartzok D. 2007. Phylogenetic review of tonal sound production in whales in relation to sociality. BMC Evol. Biol. 7:136.

McComb K, Semple S. 2005. Coevolution of vocal communication and sociality in primates. Biol. Lett. 1:381–385.

Morris-Drake A, Kern JM, Radford AN. in press. Experimental evidence for cross-modal impacts of anthropogenic noise on information use. Curr. Biol.

Mundry R, Sommer C. 2007. Discriminant function analysis with non-independent data: Consequences and an alternative. Anim. Behav. 74:965–976.

Naimi B. 2013. usdm: Uncertainty analysis for species distribution models.

Price T, Wadewitz P, Cheney D, Seyfarth R, Hammerschmidt K, Fischer J. 2015. Vervets revisited: A quantitative analysis of alarm call structure and context specificity. Sci. Rep. 5.

R Core Team. 2015. R: A Language and Environment for Statistical Computing. Vienna, Austria: R Foundation for Statistical Computing.

Rasa OAE. 1977. The Ethology and Sociology of the Dwarf Mongoose (*Helogale undulata rufula*). Z. Für Tierpsychol. 43:337–406.

Rasa OAE. 1983. Dwarf mongoose and hornbill mutualism in the Taru desert, Kenya. Behav. Ecol. Sociobiol. 12:181–190.

Rasa OAE. 1984. Mongoose Watch. London, UK: John Murray.

Rasa OAE. 1986. Coordinated vigilance in dwarf mongoose family groups: The 'watchman's song' hypothesis and the costs of guarding. Ethology 71:340–344.

Rasa OAE. 1987. The dwarf mongoose: a study of behavior and social structure in relation to ecology in a small, social carnivore. Adv. Study Behav. 17:121–163.

Rood JP. 1983. Banded mongoose rescues pack member from eagle. Anim. Behav. 31:1261–1262.

Seyfarth RM, Cheney DL, Marler P. 1980. Vervet monkey alarm calls: semantic communication in a free-ranging primate. Anim. Behav. 28:1070–1094.

Sharpe LL, Kern JM, Do Linh San E. 2015. *Helogale parvula*. IUCN red list of threatened species.

Sherman PW. 1977. Nepotism and the evolution of alarm calls. Science 197:1246–1253.

Slobodchikoff CN, Paseka A, Verdolin JL. 2009. Prairie dog alarm calls encode labels about predator colors. Anim. Cogn. 12:435–439.

Stankowich T. 2010. Risk-taking in self-defense. In: Moore J, editor. Encyclopedia of Animal Behavior. Oxford: Academic Press. p. 79–86.

Struhsaker TT. 1967. Auditory communication among vervet monkeys (*Cercopithecus aethiops*). In: Social communication among primates. Chicago, IL, USA: University of Chicago Press. p. 281–324.

Suzuki TN. 2015. Assessment of predation risk through referential communication in incubating birds. Sci. Rep. 5:10239.

Templeton C, Greene E, Davis K. 2005. Allometry of alarm calls: Black-capped chickadees encode information about predator size. Science 308:1934–1937.

Townsend SW, Rasmussen M, Clutton-Brock T, Manser MB. 2012. Flexible alarm calling in meerkats: the role of the social environment and predation urgency. Behav. Ecol. 23:1360–1364.

Venables WN, Ripley BD. 2002. Modern Applied Statistics with S. 4th ed. New York: Springer.

Wheeler BC. 2010. Production and perception of situationally variable alarm calls in wild tufted capuchin monkeys (*Cebus apella nigritus*). Behav. Ecol. Sociobiol. 64:989–1000.

Wheeler BC, Fischer J. 2012. Functionally referential signals: A promising paradigm whose time has passed. Evol. Anthropol. Issues News Rev. 21:195–205.

Zuberbühler K. 2002. A syntactic rule in forest monkey communication. Anim. Behav. 63:293–299.

Zuberbühler K. 2006. Alarm calls. In: Encyclopedia of Language & Linguistics. second edition. Oxford, UK: Elsevier. p. 143–155.

Zuberbühler K, Noë R, Seyfarth RM. 1997. Diana monkey long-distance calls: messages for conspecifics and predators. Anim. Behav. 53:589–604.

CHAPTER 4:

Meaningful Call Combinations in the Alarm Call System of Dwarf Mongooses (*Helogale parvula*): Evidence for Disjunction?

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To be submitted

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Vigilant dwarf mongoose.

ABSTRACT

Syntax, the ability to combine symbols in meaningful ways, is a fundamental property of language. However, little is known about its evolutionary origins. Comparative work represents one fruitful way to investigate this, contrasting syntax in humans to combinatorial structures in animal communication. Whilst various types of call combinations have been documented in rudimentary form in animal communication, to date, there are no known examples of combinations that resemble what is known in linguistics as disjunction. In disjunction, two or more units are combined with at least one proposition being true, but not necessarily both (*turn left* ***or*** *right*) **. Here we provide the first systematic evidence for this ability in the alarm-call system of wild dwarf mongooses (*Helogale parvula*). Observational data, acoustic analyses and playback experiments demonstrate that dwarf mongooses combine two independently meaningful alarm calls (aerial and terrestrial) into a third alarm call with a related meaning, alarm call "type-3". Type-3 alarm calls were given to various predators, both aerial and terrestrial, and natural observations and playback results indicate they function as general alarms. A linguistic analysis of production and playback data supports a disjunction-like interpretation with the combined call's most probable meaning being "(aerial or terrestrial) predator". Disjunctive combinations may represent a cognitively simple way of generalising concepts through listing alternative forms they may take. Our findings build on previous studies, demonstrating all the main types of syntactic combinations are found in rudimentary forms, and hence can and have evolved, outside of humans.**

Key-words: *Alarm call – Combinatoriality – Disjunction – Dwarf mongoose – Syntax – Vocal communication*

INTRODUCTION

Syntax, a key feature of human language, is defined as the assembly of meaningful units, such as words or morphemes, into larger meaningful sequences whose meaning is transparent (related to the meaning of its components; Jackendoff, 2002; Hurford, 2011). Syntax allows human language to generate an infinite number of messages from a finite number of words (von Humboldt, 1999). However, despite its importance for linguistic productivity, little is known about how syntax evolved. One fruitful way to study the origins of syntax is to take a comparative approach, contrasting syntax to similar features in animal communication.

In human language there are arguably four basic ways to combine meaningful structures syntactically, though they may be considered as subtypes of a single operation (Everaert et al., 2015). The first method is a predicate-argument combination in which the predicate refers to the event or state involved and the argument(s) refers to the participant(s) in the event or state (e.g. in "*Mary eats*", "*eats*" is the predicate and "*Mary*" is the argument). The second two are both types of coordination in which several units of the same type are combined into a larger unit and retain the same semantic relations with other surrounding elements (Haspelmath, 2007). In a conjunction, both propositions of the coordination are true (e.g. "*the current is strong* ***and*** *fast*"), whereas in a disjunction, at least one of the propositions is true, but not necessarily both (e.g. "*you can turn left* ***or*** *right*") (Haspelmath, 2007). The final way to combine meaningful structures is by modification in which one word, the head, is modified by another (e.g. in "*the red house*", "*red*" modifies "*house*").

Recently, comparative work has received increased research attention and combinations of meaningful calls or sound elements, which present at least superficial similarity to human syntax, have been described in several species of non-human primates, mongooses and birds. To our knowledge, there specifically exists comparable, albeit rudimentary, examples of three out of the four main types of syntactic combination in animal communication systems (see table 1). For example, banded mongoose (*Mungos mungo*) close calls consist of two segments, an initial noisy segment that carries information about the caller's identity and a second harmonic segment that carries information about the caller's activity (Jansen et al., 2012). These close calls could be considered as simple subject-predicate combinations comparable to the sentence "*I dig*" in English for example (Collier et al., 2014). Additionally, combinations similar to conjunctions have been described in two species of birds. Pied babblers (*Turdoides bicolor*) can combine their alert calls, normally produced in response to low urgency threats,

and their recruitment calls, normally used to recruit group members during locomotion, into a mobbing sequence, given to recruit group members in dangerous situations (Engesser et al., 2016). Mobbing sequences therefore inform the receiver both on the nature of the situation and the behaviour it should perform (Engesser et al., 2016). Similarly Japanese great tits (*Parus minor*) respond to ABC notes by scanning for danger and to D notes by approaching the caller (Suzuki et al., 2016). When they hear ABCD notes, they simultaneously approach the caller and scan for danger (Suzuki et al., 2016). Finally, male Campbell monkeys (*Cercopithecus campbelli*) can add a suffix "–oo" to the end of two different alarm calls: "krak", normally given to leopards, and "hok", normally given to eagles (Ouattara et al., 2009). The suffix acts as a modifier, changing the meaning of both calls from that of a specific predator to a more general alarm call (Collier et al., 2014; Ouattara et al., 2009), eliciting a weaker response in receivers than the non-suffixed call (Coye et al., 2015).

Table 1: Examples of combinations of meaningful calls in animal communication.

Species	Reference	Individual calls/elements (1)	Individual calls/elements (2)	Combination	Type of combination
Campbell monkey *Cercopithecus campbelli*	Ouattara et al., 2009	"krak" (leopard), "hok" (eagle)	"-oo" (modifier)	"krak-oo" (general disturbance), "hok-oo" (general disturbance in the canopy)	Modification
Putty-nosed monkey *Cercopithecus nictitans martini*	Arnold and Zuberbühler, 2012, 2006	"pyow" (leopard)	"hack" (eagle)	"pyow-hack sequence" (group movement)	Idiomatic combination
Banded mongoose *Mungos mungo*	Jansen et al., 2012	Initial noisy segment (caller identity)	Harmonic segment (caller activity)	Close call (caller identity + activity)	Argument + predication
Meerkat *Suricata suricatta*	Manser et al., 2014	Terrestrial alarm (terrestrial predator)	Moving animal call (moving animal)	Terrestrial + moving animal alarm (moving terrestrial predator)	Conjunction: precision on type/level of threat
Pied babbler *Turdoides bicolor*	Engesser et al., 2016	Alert call (low level threat)	Recruitment call (approach the caller)	Mobbing call (approach the caller when there is a low level threat)	Conjunction: Context + requested action
Japanese great tit *Parus minor*	Suzuki et al., 2016	ABC notes (scan for danger)	D notes (approach caller)	ABCD notes (scan for danger + approach caller)	Conjunction: Two simultaneously requested actions

However, to date, no examples of disjunction have been described in animal communication systems. This is particularly surprising given that disjunction can be considered as the cognitively simplest way of generalisation and concept formation (pers. comm. S. Stoll), which it does by listing the possible alternatives of a concept. In this study we provide data demonstrating that dwarf mongooses produce alarm call combinations that can potentially be interpreted as a form of disjunction.

Dwarf mongooses are small, social African carnivores. They live in groups of up to 30 individuals (Rasa, 1977), composed of a dominant pair and subordinate individuals of both sexes, both related and unrelated to the dominant male and female (Keane et al., 1994). They forage for insects and small vertebrates as part of a group. During foraging, an individual often performs sentinel behaviour, standing in an elevated position and alerting the rest of the group to threats by producing alarm calls (Rasa, 1986). Dwarf mongooses have a large repertoire of alarm calls, including two predator specific alarm calls given to aerial and terrestrial predators (Collier et al., in review). Previous work documenting dwarf mongoose alarm calls shows that one alarm call, type 3 (hereafter, T_3), appears to be a combination of aerial and terrestrial alarm calls (figure 1; Collier et al., in review). Using a combination of acoustic analyses, observational data and playback experiments, we systematically tested whether this was the case.

Specifically, we examined whether T_3 was indeed a combination of an aerial and a terrestrial alarm call by comparing the acoustic parameters of the individual alarm calls to those of the two component parts of T_3. Furthermore, we investigated whether mongooses perceived T_3 as a combination by comparing their reaction to the individual alarm calls in relation to their responses to the two component parts of T_3. Natural observations, predator presentations and playback experiments were then implemented to establish the function of T_3. Finally, based on these results, we proposed possible linguistic interpretations of dwarf mongoose alarm call combinations.

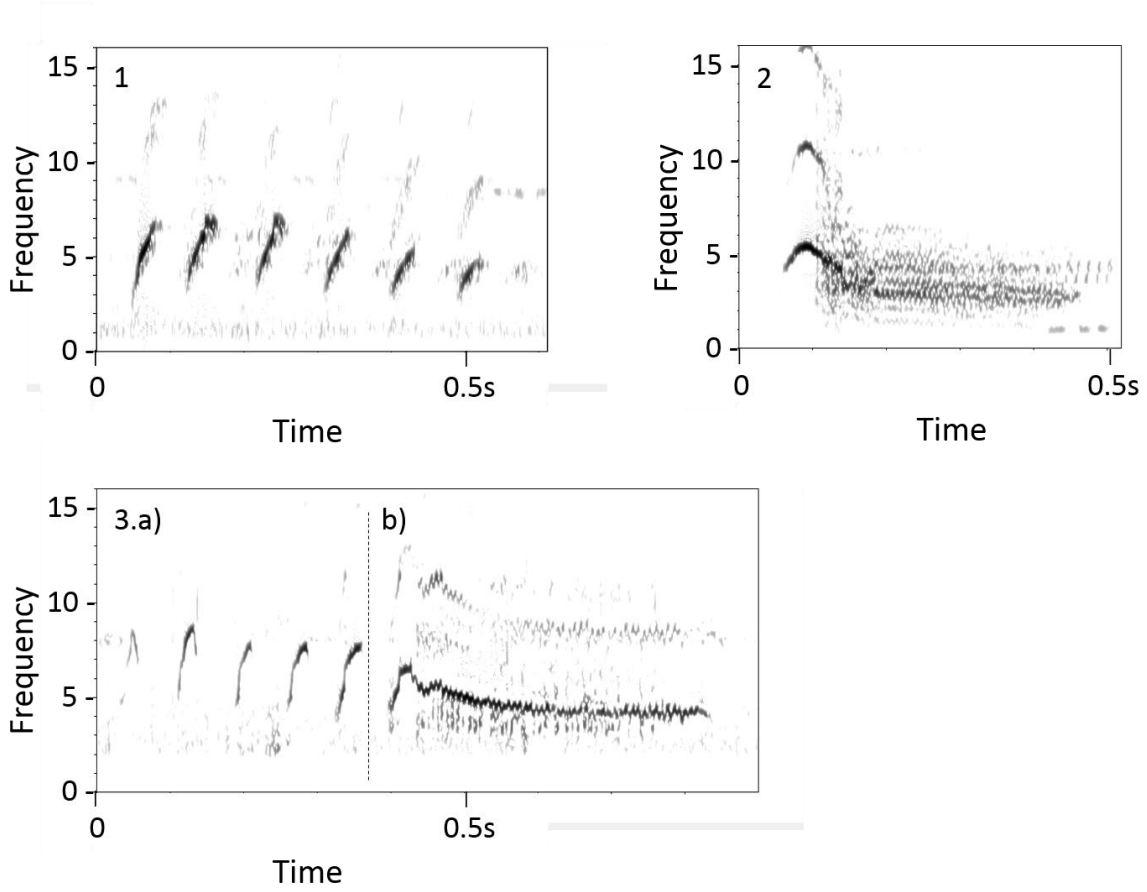

Figure 1: Spectrograms of dwarf mongoose alarm calls. 1) Aerial alarm call; 2) Terrestrial alarm call; 3) T_3 alarm call composed of two parts: a) pulsed first segment ($T_{3.1}$) and b) noisy second segment ($T_{3.2}$).

METHODS

Study site and population

Our research was carried out on Sorabi Rock Lodge, a private game reserve in Limpopo province, South Africa (for a more detailed description see Kern & Radford, 2013). Data were collected over two field seasons (November 2014 – June 2015; January – February 2016) from mongooses over a year of age. These mongooses belonged to 7 wild but habituated groups composed of 6 to 15 individuals (mean group size = 11). Individuals were habituated to close observations and would allow recordings from a distance of less than 5 meters. All mongooses were individually identifiable by small blonde dye-marks or distinguishable features such as scars.

Alarm call production

Mongoose groups were followed for three hours in the morning after they left their sleeping burrow and another two to three hours in the evening before they returned to a sleeping burrow. Their vocalisations were recorded ad libitum using a Marantz PMD661 MKII solid state recorder (D&M Holding, Inc., Kanagawa, Japan; sampling rate 44.1; 24 bit accuracy) attached to a Sennheiser ME66/K6 directional microphone (Sennheiser Electronic Corp., Old Lyme, CT, U.S.A.). Whenever an alarm call was produced, its location was marked on the soundtrack and, where possible, the caller's identity, the stimulus the call was given to and the group's reaction to the alarm call were noted. To obtain additional alarm calls, we also carried out experimental predator presentations, using a helium balloon and a domestic dog (*Canis lupus familiaris*) to simulate an aerial and terrestrial predator respectively (for more details, see Collier et al., in prep.).

Acoustic analysis

In order to test whether the structure of type 3 alarm calls (T_3) is a combination of aerial and terrestrial alarms, we carried out an acoustic analysis. Using acoustic analysis software Praat version 5.3.85 (www.praat.org), we selected good quality alarm calls with a high signal to noise ratio for the analysis. Using Luscinia (Lachlan, 2007) we then extracted several temporal and spectral parameters from the selected calls (see table 2). We did this for each of the natural alarm call types (aerial, terrestrial and T_3 alarm calls) but also for the pulsed first half of T_3 ($T_{3.1}$) and the noisy second half of T_3 ($T_{3.2}$).

Playbacks

For all playbacks, we selected calls with a good signal to noise ratio as stimuli, providing 15 exemplars of aerial, 12 of terrestrial and 9 of T_3 alarm calls. We only used stimuli recorded from a foreign group to avoid the focal hearing its own alarm call during the experiment and we played back the alarm calls from a height of about 1 meter to simulate a call from an individual on sentinel. For both sets of experiments, playbacks took place when the focal mongoose was foraging in the open and its response was filmed using a handheld camcorder. We noted the focal individual's strongest response to the playback and, as with our previous work on dwarf mongooses, scored its strength as 1= no reaction, 2=vigilance, 3=moved and

4=ran for cover (Collier et al., in prep.). We also determined the focal's latency to resume normal behaviour. Furthermore, we noted whether the mongoose performed additional anti-predator behaviours within the minute following the playback, such as looking at the sky which may allow it to detect aerial predators, or beginning a sentinel bout which could allow it to detect any type of predator. Experiments only took place if no conspecific or heterospecific alarm calls had been heard within the last 10 minutes and the mongooses were showing no signs of alarm or arousal from a previous event (predator encounter or intergroup interaction). At least an hour separated two successive playbacks, with a maximum of three playbacks per session (morning or afternoon).

a) Natural alarm calls

To investigate whether dwarf mongooses reacted differently to the three natural alarm calls, we played back aerial and terrestrial alarm calls to 17 focal adult mongooses each, from 7 different groups. For each stimulus, one individual out of the 17 was tested twice, giving a total of 18 playbacks for these two alarm calls. Moreover, we played back T_3 alarm calls to 14 individuals belonging to 7 different groups. One individual was tested twice, before and after emigrating to a new group, giving a total of 15 playbacks of T_3 alarm calls.

b) Paired natural and manipulated alarm calls

To test whether dwarf mongooses perceived T_3 alarm calls as combinations of aerial and terrestrial alarm calls, we carried out paired playbacks of three sets of stimuli: i) T_3 and artificial T_3 alarms (T_{3art}), created by pasting an aerial and a terrestrial alarm together, ii) aerial and $T_{3.1}$ alarm calls and iii) terrestrial and $T_{3.2}$ alarm calls. Each pair of stimuli was played back to 10 focal mongooses belonging to 7 different groups, however set i) could only be played back to 8 out of the 10 individuals. Whenever possible paired playbacks were performed on the same day, if this was not feasible, they were carried out on consecutive days.

Table 2: Measured acoustic parameters and their definitions.

Acoustic parameter	Description
Call length	Time elapsed between the beginning and the end of the call.
Overall peak frequency	Peak frequency is the frequency of maximum amplitude within one spectrum of the spectrogram. Overall peak frequency is the frequency of maximum amplitude within the call.
Mean peak frequency	Mean of all peak frequencies within the call.
Maximum peak frequency	Peak frequency of highest peak frequency within the call.
Minimum peak frequency	Peak frequency of the lowest peak frequency within the call.
Mean fundamental frequency	Fundamental frequency is the lowest frequency of a periodic waveform.
Maximum fundamental frequency	Fundamental frequency of highest frequency within the call.
Minimum fundamental frequency	Fundamental frequency of lowest frequency within the call.
Mean change in peak frequency	Mean change in peak frequency over time.
Mean change in fundamental frequency	Mean change in fundamental frequency over time.
Mean Wiener entropy	A measure of noisiness: Ratio of the geometric mean to the arithmetic mean of the power spectrum.
Mean frequency bandwidth	Frequency difference between the first and final maximum intensity in the signal.
Number of elements	Number of continuous traces on the spectrogram that compose the call.
Within syllable gap	Total duration of silence between the elements of a call.

Statistical analysis

a) Acoustic analysis

We compared the three natural calls to each other as well as aerial and terrestrial alarm calls to $T_{3.1}$ and $T_{3.2}$ respectively using the measured acoustic parameters. We started by removing any collinear parameters, as determined by their variance inflation factors (VIF). We calculated VIFs for all parameters and discarded the parameter with the highest VIF and then repeated these steps until all remaining parameters had VIFs with values lower than 10 and therefore should not be collinear (Belsley et al., 2005). We then used the remaining parameters to run a permutated discriminant function analysis (pDFA) using a function provided by R. Mundry. Unlike conventional DFAs, pDFAs allow for repeated measures due to multiple recordings of an individual or group and do not return inflated p-values (Mundry and Sommer, 2007). All analyses were performed using R version 3.2.1 (R core team, 2015) with the packages usdm (Naimi, 2013) and MASS (Venables and Ripley, 2002).

b) Natural alarm call playbacks

We investigated the subjects' strength of reaction when hearing the different natural alarm calls using Cumulative Link Mixed Models (CLMM). When a significant result was returned, we carried out post-hoc pairwise CLMMs between the treatments (aerial vs T_3, terrestrial vs T_3, aerial vs terrestrial). P-values were adjusted for multiple testing using Bonferroni's correction. To compare latencies to relax in response to the different stimuli we carried out Linear Mixed Models (LMM). Our data did not violate the assumptions of linearity, homoscedasticity and normality of the residuals. We performed Generalized Linear Mixed Models (GLMM) with a binomial family and a logit link function to test whether the expression of the additional anti-predator behaviours (looking up and going on sentinel) differed in response to the different playbacks. For all the models, we fitted stimulus type (aerial, terrestrial or T_3 alarm call) as fixed effect. Furthermore, as some individuals were tested more than once and that multiple individuals from the same group were used as subjects, we fitted individual nested within group as random factor. P-values were obtained using likelihood ratio tests comparing full models, including all the explanatory variables, to reduced models including the same explanatory variables but without the variable of interest. Analyses were performed using R with the packages ordinal (Christensen, 2015) and lme4 (Bates et al., 2015).

c) Paired natural and manipulated alarm call playbacks

We compared subjects' strength of reaction and latency to relax in reaction to a natural alarm call and its corresponding artificial alarm call using Wilcoxon signed rank tests. We compared the expression of looking up and sentinel behaviours using GLMMs with a binomial family and a logit link function. Stimulus type was fitted as fixed effect, with group as random effect and p-values were calculated using likelihood ratio tests. Statistics were carried out using R and the package lme4.

Ethical Note

Our work was carried out under permission from the Limpopo Department of Economic Development, Environment and Tourism (permit number: 001-CPM403-00013) and the Ethical Committee of Pretoria University, South Africa (permit number: EC049-16).

RESULTS

Acoustic analysis

The three natural alarm call types, aerial, terrestrial and T_3 alarm calls, were distinguishable by their acoustic parameters (pDFA, p=0.001, percentage correctly cross classified=80%). When comparing aerial and terrestrial alarm calls with the corresponding sections of T_3 alarm calls, statistical analysis revealed that aerial and $T_{3.1}$ alarm calls could not be distinguished by the measured acoustic parameters alone (pDFA, p=0.091, percentage correctly cross classified=68%). On the contrary, terrestrial and $T_{3.2}$ alarm calls could be discriminated using those acoustic parameters (pDFA, p=0.026, percentage correctly cross classified=94%) (figure 2).

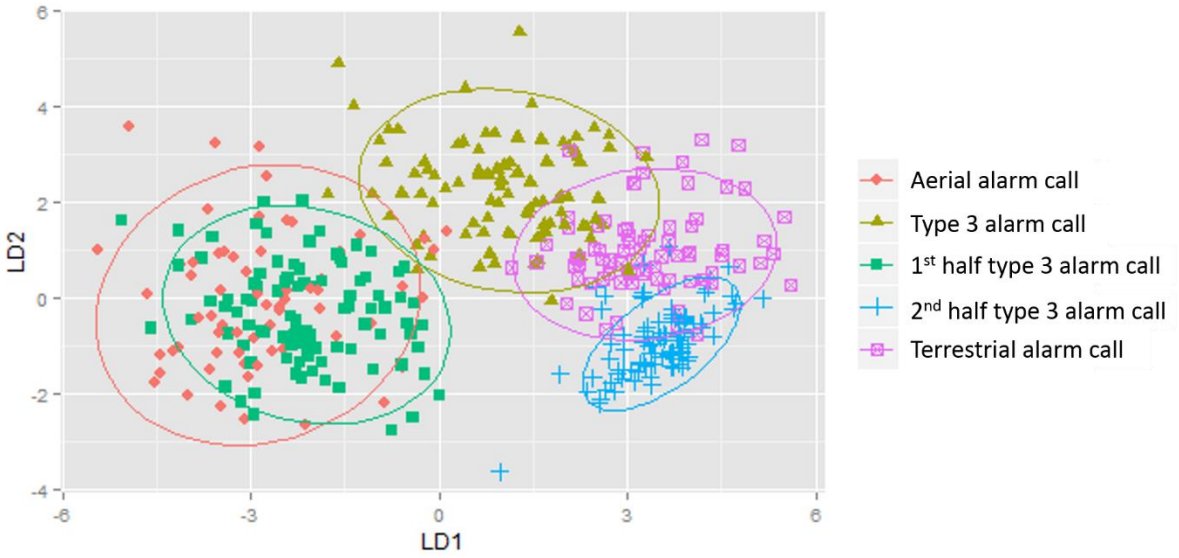

Figure 2: Output of DFA showing the distribution of discriminant scores along the two principal discriminant functions. LD: linear discriminant function.

Context of production of T_3 alarm calls

During natural encounters with predators, T_3 alarm calls were mainly given in response to aerial stimuli (124 out of 159 T_3 alarm calls produced in natural situations), but were also given to banded mongooses (27 calls) and, very occasionally (1-3 calls), to antelope, primates, heterospecific alarm calls, perched birds and scents. Moreover, T_3 alarm calls were often produced in response to the observer (145 out of 588 calls given to the observer). During predator presentations, T_3 alarm calls were given both to the dog and the helium balloon, albeit in different proportions. For the dog presentations, 48 out of 280 alarm calls produced were T_3 alarm calls, whereas for the helium balloon presentations 216 out of 478 calls were T_3 alarm calls. Table 3 gives a simplified overview of the contexts of production of all three natural alarm calls: T_3, aerial and terrestrial.

Table 3: Simplified contexts in which the different alarm calls were produced, both during natural encounters and predator presentations.

	Natural encounters			**Predator presentations**			**Observer**
	Aerial stimuli	Scents	Total recorded	Helium balloon	Dog	Total	Observer
Aerial alarm calls	272	0	301	197	2	199	73
Terrestrial alarm calls	10	235	255	0	194	194	199
T_3 alarm calls	124	1	159	216	48	264	145

Playback of natural alarm calls

Subjects' strength of reaction depended on alarm call type (CLMM, df=2, χ^2=6.88, p=0.03). Pairwise comparisons showed that strength of reaction was the same in response to aerial and T_3 alarm calls (CLMM, df=1, χ^2=1.27, Bonferroni adjusted p=0.78) and to terrestrial and T_3 alarm calls (CLMM, df=1, χ^2=2.01, Bonferroni adjusted p=0.48). However subjects reacted more strongly to aerial than to terrestrial alarm calls (CLMM, df=1, χ^2=7.01, Bonferroni adjusted p=0.024), running for cover more often in response to aerial alarms (12 out of 18 trials) and engaging in vigilance more often in response to terrestrial alarm calls (12 out of 18 trials) (figure 3). There was no overall significant difference in latency to relax (LMM, df=2, χ^2=1.90, p=0.39), sentinel behaviour (GLMM, df=2, χ^2=0.28, p=0.87) or looking up behaviour (GLMM, df=2, χ^2=4.98, p=0.083) in response to the three different alarm calls. However, pairwise comparisons showed that there was a trend for looking up behaviour to differ between aerial and T_3 alarm calls (GLMM, df=1, χ^2=3.38, p=0.066) and no looking up behaviours at all were produced in reaction to terrestrial alarm calls (figure 4).

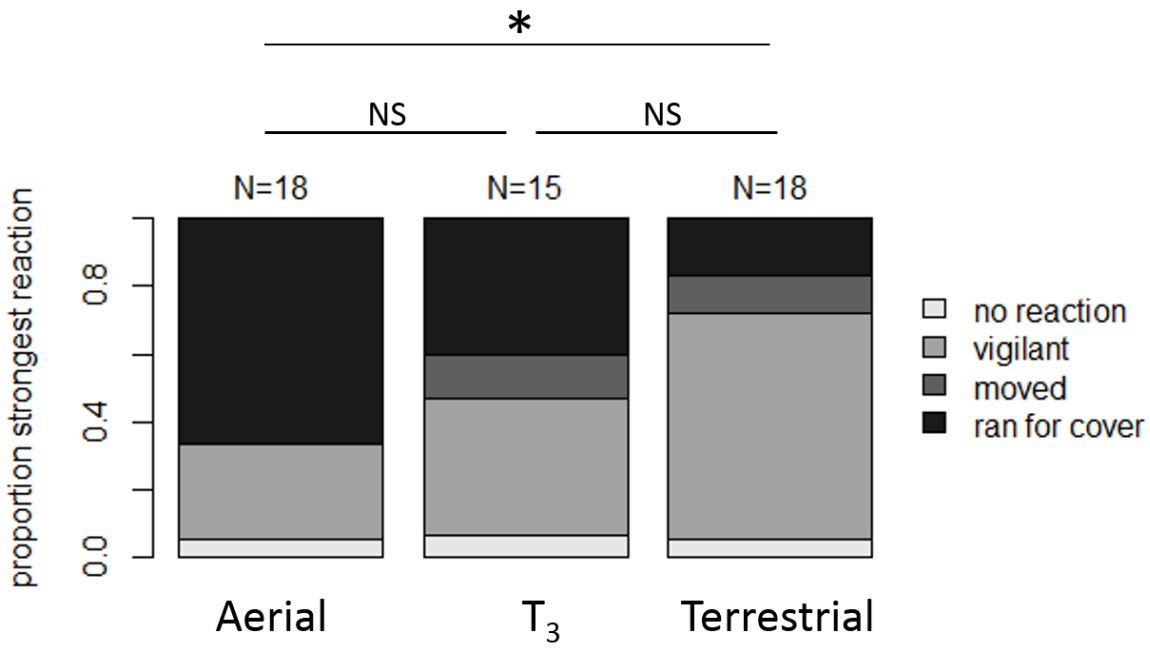

Figure 3: Strength of focal individuals' reactions to the playbacks of natural alarm calls.

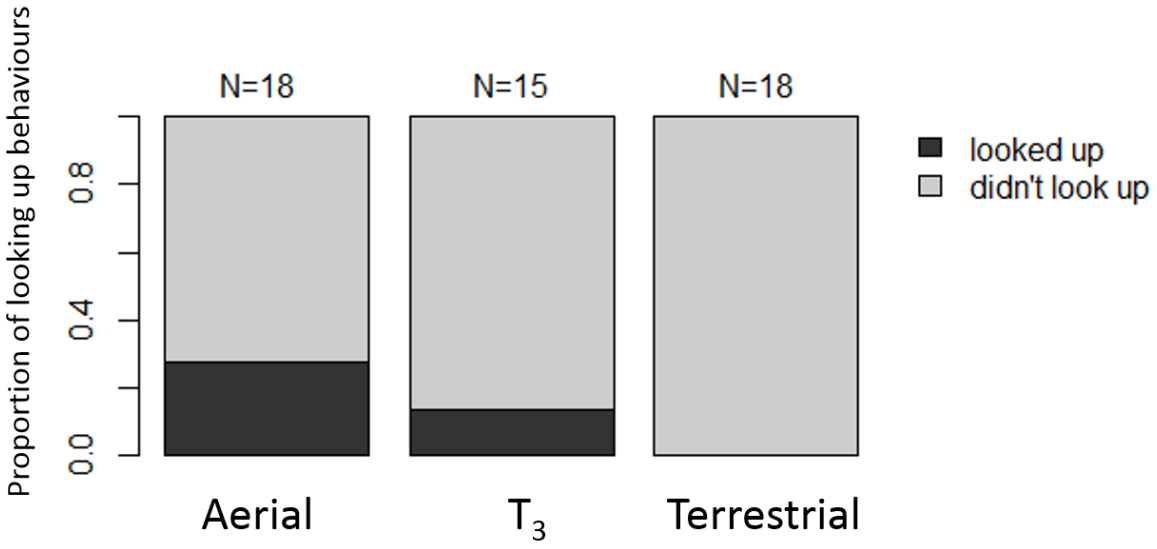

Figure 4: Subjects' looking up behaviour in response to playbacks of natural alarm calls.

Playback of paired natural and experimentally modified alarm calls

When comparing subjects' reactions to natural alarm calls and their artificial counterparts we found no difference. Strength of reaction did not differ significantly in response to aerial and $T_{3.1}$ alarm calls (Wilcoxon, v=6, p=0.18), to terrestrial and $T_{3.2}$ alarm calls (Wilcoxon, v=14, p=0.52) or to T_3 and T_{3art} alarm calls (Wilcoxon, v=6.5, p=0.46) (figure 5). There was also no difference in latency to relax between the pairs of playbacks (Wilcoxon: aerial and $T_{3.1}$, v=21, p=0.73; terrestrial and $T_{3.2}$, v=12, p=0.83; T_3 and T_{3art}, v=16.5, p=0.51) or in sentinel (GLMM: aerial and $T_{3.1}$, df=1, χ^2=1.41, p=0.23; terrestrial and $T_{3.2}$, df=1, χ^2=0.43, p=0.51; T_3 and T_{3art}, df=1, χ^2=0.40, p=0.53) or looking up behaviours (GLMM: aerial and $T_{3.1}$, df=1, χ^2=0, p=1; T_3 and T_{3art}, df=1, χ^2=0, p=1).

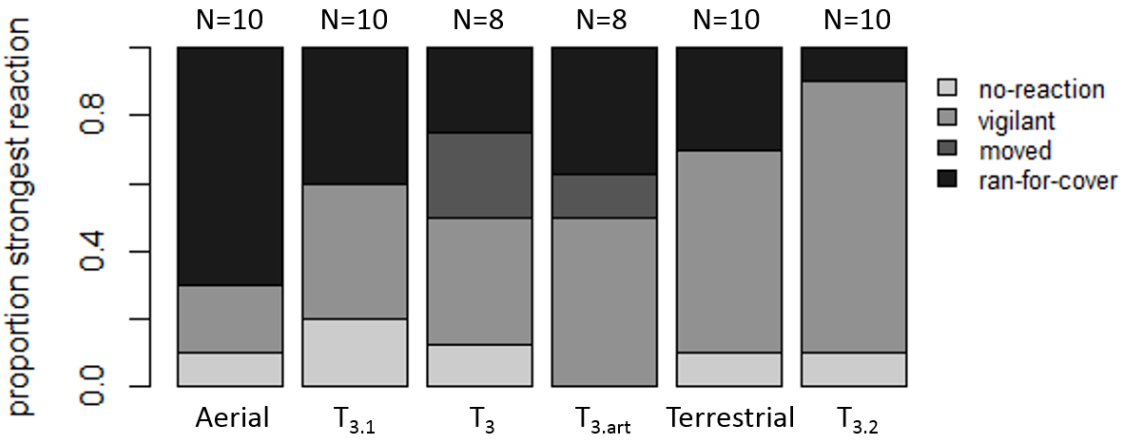

Figure 5: Subjects' strength of reaction in response to playbacks of natural alarm calls and their corresponding artificially obtained alarm calls.

DISCUSSION

Our results show that dwarf mongooses combine two meaningful alarm calls into a third alarm call with a related meaning. The responses to the paired playbacks of the individual calls and the different parts of T_3 indicate that T_3 is indeed a combination despite differences in acoustic structure between $T_{3.2}$ and terrestrial alarm calls. $T_{3.2}$'s differing acoustic structure is therefore likely to result from co-articulation, in which the properties of a sound are modified by the influences of adjacent sounds (Gandour et al., 1992), due to being preceded by $T_{3.1}$.

Analysing the information content of animal call combinations is non-trivial. One particular complication is that the meaning attributed to the individual component calls may be ambiguous or vague (Macedonia and Evans, 1993). Functionally referential alarm calls in animal species, for example, could potentially refer to the type of predator constituting the threat (declarative; e.g. raptor) (Seyfarth et al., 1980), its location (e.g. in the air) (Zuberbühler, 2000) or the type of anti-predator behaviour the receiver should perform (imperative; e.g. run for cover) (Macedonia and Evans, 1993).

Consequently, in this study, we considered multiple interpretations of the meaning of T_3 depending on the potential informational content of the aerial and terrestrial alarm calls (see

table 4). The majority of these interpretations can be rejected as improbable based on the results from the production data and playback experiments. Nevertheless, two potential interpretations remain, one more plausible than the other. In the first, less probable, interpretation, the individual alarm calls indicate the behaviour the receivers should perform: run for cover for the aerial alarm and vigilance for the terrestrial alarm. In this case, T_3 would then convey something akin to "run for cover and be vigilant". Whilst possible, this interpretation is problematic, primarily because experimental data suggest dwarf mongooses will sometimes become vigilant in response to an aerial alarm call or run for cover in response to a terrestrial alarm call. Furthermore, mongooses sometimes only perform one and not both of these behaviours when hearing a T_3 alarm call. In the second, more probable, interpretation, the aerial and terrestrial alarm calls refer respectively to aerial and terrestrial predators and T_3 refers in a general way to an aerial or terrestrial predator (but not both at the same time). This interpretation would represent a disjunction analysis.

The disjunction interpretation best fits the data from both production and perception aspects. Whereas aerial alarm calls are given to aerial stimuli, helium balloons and observers and terrestrial alarm calls are given to dogs, secondary cues of predator presence and observers, T_3 is produced in response to of all these stimuli with the exception of secondary cues (table 5). The production of T_3 in a broad range of situations seems to confirm its function as a general alarm call, possibly used when the caller lacks specific information on the threat. This seems to be corroborated by the production of T_3 in relatively high numbers in response to observers and helium balloons. Observers potentially represent an ambiguous stimuli as, despite being on the ground, their close proximity to the mongooses may mean subjects sometimes perceive them as being aerial. Helium balloons may also constitute ambiguous stimuli because, despite being clearly aerial, they do not resemble any other threat in the mongooses' habitat. From the comprehension side, whilst mongooses' strength of reaction to aerial and terrestrial alarm calls differs significantly, their reactions to T_3 can involve the primary reaction to one or the other of these two calls and are not significantly different from those of either (table 5). Mongooses also scan the sky in response to T_3, but not as often as in response to an aerial alarm call. This range of behaviours would be consistent with a general alarm call. As the caller does not specify the type of danger, each individual receiver must evaluate the level of danger and react accordingly. Exactly how the level of danger is perceived by the receiver may be affected by various factors, both internal and external, including hunger levels, foraging investment (Amsler, 2007; Manser et al., 2014) or perhaps caller reliability (Cheney and Seyfarth, 1988).

Table 4: Possible interpretations of dwarf mongoose T_3 alarm call combinations depending on the meaning of the individual calls.

Meaning aerial alarm call	Meaning terrestrial alarm call	Meaning T_3 alarm call	Linguistic term for combination	Likelihood of interpretation	Explanation
Predator in the air	Predator on the ground	Predator between the air and the ground (in the trees)	Blend	Unlikely	- Predators normally in the air or on the ground, very rarely seen in the trees, whereas T_3 calls are common. - T_3 alarm calls are given to both predators in the air (aerial) and on the ground (terrestrial).
Aerial predator	Terrestrial predator	Aerial and terrestrial predators present at the same time	Conjunction	Unlikely	- This combination of events was not seen in seven months of observation, whereas T_3 calls are common. - We would expect a stronger reaction to T_3 rather than an intermediate one if more than one type of predator was present at once.
Aerial predator	Terrestrial predator	(Aerial or terrestrial) predator	Disjunction	Likely	- This interpretation is consistent with both the mongooses' reactions to playbacks and the contexts of production of the alarm calls (see table 5).
High urgency threat	Low urgency threat	Intermediate urgency threat	Blend	Unlikely	- Here, we would expect aerial alarm calls to be given to terrestrial predators when they represent a high urgency threat and terrestrial alarm calls to be given to aerial predators when they are a low urgency threat. However this is very rarely the case (see table 3).
Run for cover	Be vigilant	Run for cover and be vigilant	Conjunction	Possible	- Consistent with most frequent reactions to the alarm calls but mongoose sometimes run for cover in response to a terrestrial alarm call and go vigilant in response to an aerial one (see figure 3).
Aerial predator	Be vigilant	Be vigilant, (low urgency) aerial predator	Modification	Unlikely	- T_3 alarm calls are given to terrestrial predators and observers as well as to aerial predators. - Requires higher cognitive abilities than simple conjunction.
Aerial predator	Low urgency threat	Low urgency aerial predator	Modification	Unlikely	- T_3 alarm calls are given to terrestrial predators and observers as well as to aerial predators. - Requires higher cognitive abilities than simple conjunction.
Run for cover	Terrestrial predator	Run for cover, (high urgency) terrestrial predator	Modification	Unlikely	- Most naturally recorded T_3 alarm calls are given to aerial predators. - Requires higher cognitive abilities than simple conjunction.
High urgency threat	Terrestrial predator	High urgency terrestrial predator	Modification	Unlikely	- Most naturally recorded T_3 alarm calls are given to aerial predators. - Requires higher cognitive abilities than simple conjunction.
High urgency, aerial, threat	Lower urgency, terrestrial, threat	Intermediate urgency, (aerial or terrestrial) threat	Blend & Disjunction	Highly unlikely	- This interpretation is not parsimonious and would require high cognitive abilities.

Whilst general alarm calls are common in animal species, it is still unclear why dwarf mongooses use a combination of independently occurring calls to fulfil this function. It has been hypothesised that compositional systems should evolve when there are more events to communicate than individual calls present in the repertoire (Nowak et al., 2000; Nowak and Krakauer, 1999). This is supported by some research on animal combinatorial systems (e.g. pied babblers: Engesser et al., 2016). Yet dwarf mongooses produce 11 different types of alarm calls, of which 5 are very rarely produced and whose function is unclear (Collier et al., in prep.). Why a combination of initially existing calls is produced over an individual call type is therefore unclear. In line with modelling work, it is possible that each of the individual alarm calls accomplishes a precise and specific function, leading to the concatenation of calls to communicate additional information (Nowak et al., 2000). Moreover, disjunctive combinations may represent a cognitively simple way of generalising a concept, potentially making them relevant general alarm calls. In the case of T_3 calls, dwarf mongooses generalise their alarm call by listing the alternative forms a predator may take: aerial predator or terrestrial predator.

To our knowledge, this is the first example of a potential disjunctive combination in animal communication. Our research furthers existing comparative work demonstrating potential homologous or analogous examples of predicate-argument, conjunction and modification by showing that all four main types of combinations in human language are implemented in rudimentary forms in various animal species' communication systems. Moreover, several of these examples of combinatoriality come from non-primate species, more distantly related to humans, suggesting that the ability to combine meaningful calls has evolved independently in these different species. Further comparative work could inform us on the relative distribution of these forms of combinatoriality across species and taxa. It could also lead to a better understanding of the possible social and environmental factors selecting for the use of these combinatorial abilities and whether different the types of combination (predicate-argument, conjunction, disjunction and modification) are favoured by different factors.

Table 5: Contexts of production and principal reactions in response to the two individual alarm calls and their combination, T_3.

	Production in response to					**Main response when hearing alarm call**		
	Aerial stimuli	Helium balloon	Dog	Secondary cues	Observer	Run for cover	Vigilance	Look at the sky
Aerial alarm call	**x**	**x**			**x**	**x**		**x**
Terrestrial alarm call			**x**	**x**	**x**		**x**	
T_3 alarm call	**x**	**x**	**x**		**x**	**x**	**x**	**x**

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REFERENCES

Amsler, V., 2007. How urgency levels in alarm calls influence the forager's response in meerkats (*Suricata suricatta*) (MSc). University of Zurich, Zurich, Switzerland.

Bates, D., Meachler, M., Bolker, B.M., Walker, S., 2015. lme4: Linear mixed-effects models using Eigen and S4.

Belsley, D.A., Kuh, E., Welsch, R.E., 2005. Regression diagnostics: Identifying influential data and sources of collinearity. John Wiley & Sons, New York, NY, USA.

Cheney, D.L., Seyfarth, R.M., 1988. Assessment of meaning and the detection of unreliable signals by vervet monkeys. Anim. Behav. 36, 477–486. doi:10.1016/S0003-3472(88)80018-6

Christensen, R.H.B., 2015. Ordinal - Regression Models for Ordinal Data.

Christiansen, M.H., Kirby, S., 2003. Language evolution: consensus and controversies. Trends Cogn. Sci. 7, 300–307.

Collier, K., Bickel, B., van Schaik, C.P., Manser, M.B., Townsend, S.W., 2014. Language evolution: syntax before phonology? Proc. R. Soc. B Biol. Sci. 281. doi:10.1098/rspb.2014.0263

Collier, K., Radford, A.N., Townsend, S.W., Manser, M.B., in prep. Wild dwarf mongooses produce both urgency related and predator-specific alarm calls.

Coye, C., Ouattara, K., Zuberbuhler, K., Lemasson, A., 2015. Suffixation influences receivers' behaviour in non-human primates. Proc. R. Soc. B Biol. Sci. 282, 20150265–20150265. doi:10.1098/rspb.2015.0265

Engesser, S., Ridley, A.R., Townsend, S.W., 2016. Meaningful call combinations and compositional processing in the southern pied babbler. Proc. Natl. Acad. Sci. 201600970.

Everaert, M.B.H., Huybregts, M.A.C., Chomsky, N., Berwick, R.C., Bolhuis, J.J., 2015. Structures, not strings: linguistics as part of the cognitive sciences. Trends Cogn. Sci. 19, 729–743.

Gandour, J., Potisuk, S., Dechongkit, S., Ponglorpisit, S., 1992. Tonal coarticulation in Thai disyllabic utterances: a preliminary study. Linguist. Tibeto-Burman Area 15, 93–110.

Haspelmath, M., 2007. Coordination, in: Shopen, T. (Ed.), Language Typology and Syntactic Description. Cambridge University Press, Cambridge, UK, pp. 1–51.

Hockett, C.F., 1960. The origin of speech. Sci. Am. 203, 88–111.

Hurford, J.R., 2011. The origins of grammar: Language in the light of evolution II. Oxford University Press, Oxford, UK.

Jackendoff, R., 2002. Foundations of language: brain, meaning, grammar, evolution. Oxford University Press, Oxford, UK.

Jansen, D.A.W.A.M., Cant, M.A., Manser, M.B., 2012. Segmental concatenation of individual signatures and context cues in banded mongoose (*Mungos mungo*) close calls. BMC Biol. 10, 97. doi:10.1186/1741-7007-10-97

Keane, B., Waser, P.M., Creel, S.R., Creel, N.M., Elliott, L.F., Minchella, D.J., 1994. Subordinate reproduction in dwarf mongooses. Anim. Behav. 47, 65–75.

Kern, J.M., Radford, A.N., 2013. Call of duty? Variation in use of the watchman's song by sentinel dwarf mongooses, *Helogale parvula*. Anim. Behav. 85, 967–975. doi:10.1016/j.anbehav.2013.02.020

Macedonia, J.M., Evans, C.S., 1993. Essay on contemporary issues in ethology: Variation among mammalian alarm call systems and the problem of meaning in animal signals. Ethology 93, 177–197. doi:10.1111/j.1439-0310.1993.tb00988.x

Manser, M.B., Jansen, D.A.W.A.M., Graw, B., Hollén, L.I., Bousquet, C.A.H., Furrer, R.D., le Roux, A., 2014. Vocal complexity in meerkats and other mongoose species, in: Advances in the Study of Behavior. Elsevier, pp. 281–310.

Mundry, R., Sommer, C., 2007. Discriminant function analysis with nonindependent data: Consequences and an alternative. Anim. Behav. 74, 965–976. doi:10.1016/j.anbehav.2006.12.028

Naimi, B., 2013. usdm: Uncertainty analysis for species distribution models.

Nowak, M.A., Krakauer, D.C., 1999. The evolution of language. Proc. Natl. Acad. Sci. 96, 8028–8033. doi:10.1073/pnas.96.14.8028

Nowak, M.A., Plotkin, J.B., Jansen, V.A.A., 2000. The evolution of syntactic communication. Nature 404, 495–498. doi:10.1038/35006635

Ouattara, K., Lemasson, A., Zuberbühler, K., 2009. Campbell's monkeys use affixation to alter call meaning. PloS One 4, e7808. doi:10.1371/ journal.pone.0007808

Rasa, O.A.E., 1986. Coordinated vigilance in dwarf mongoose family groups: The "watchman"s song' hypothesis and the costs of guarding. Ethology 71, 340–344. doi:10.1111/j.1439-0310.1986.tb00598.x

Rasa, O.A.E., 1977. The Ethology and Sociology of the Dwarf Mongoose (*Helogale undulata rufula*). Z. Für Tierpsychol. 43, 337–406. doi:10.1111/j.1439-0310.1977.tb00487.x

Seyfarth, R.M., Cheney, D.L., Marler, P., 1980. Vervet monkey alarm calls: semantic communication in a free-ranging primate. Anim. Behav. 28, 1070–1094.

Suzuki, T.N., Wheatcroft, D., Griesser, M., 2016. Experimental evidence for compositional syntax in bird calls. Nat. Commun. 7, 10986. doi:10.1038/ncomms10986

Venables, W.N., Ripley, B.D., 2002. Modern Applied Statistics with S, 4th ed. Springer, New York.

von Humboldt, W., 1999. On language: on the diversity of human language construction and its influence on the mental development of the human species. Cambridge University Press, Cambridge, UK.

Zuberbühler, K., 2000. Referential labelling in Diana monkeys. Anim. Behav. 59, 917–927. doi:10.1006/anbe.1999.1317

GENERAL DISCUSSION:

Dwarf mongoose with its group.

In this thesis, I investigated the emergence of combinatoriality from a comparative perspective. Re-analysing examples of animal call combinations from the literature using insights from the field of linguistics, I showed that syntax-like combinations appeared to be more widespread in animal communication than phonology-like sequences, suggesting that syntax may have evolved before phonology. I then empirically investigated specific aspects of combinatoriality in two species of social mongooses: call combinations in social and in predation contexts. I showed that call combinations play an important role in meerkat (*Suricata suricatta*) social communication, and that dwarf mongooses (*Helogale parvula*) use a combination of two independent alarm calls as a general alarm.

Call Combinations in Social Mongooses

Here, I showed that meerkats produce twelve call combinations across eight behavioural contexts in social situations (chapter 2). These combinations varied in length as well as in structural type and complexity, with all four structural classes of combination represented: finite and unlimited repetitions, and discrete and graded mixed combinations. Some call combinations were exclusive to a particular behavioural context but the majority were emitted in more than one behavioural context in varying proportions. This diversity of combinations and their broad use across social situations suggests the importance of call combinations in social communication for meerkats. Future work is needed to investigate the function of these combinations and how it differs from that of their component calls, focussing in particular on how receivers perceive and process these combinations. This would offer a more comprehensive understanding of the use of social call combinations in meerkat communication.

A second key aspect of this thesis was the study of dwarf mongoose alarm call combinations (chapter 4). I first showed that dwarf mongooses produce, among others, predator specific alarm calls in response to aerial and terrestrial threats (chapter 3). I then examined how dwarf mongooses combined these two meaningful calls into a third alarm call, T_3, with a related meaning. T_3 appears to be a general alarm call whose meaning can be interpreted as "(aerial or terrestrial) predator". T_3 therefore appears to be the first example of a disjunction-like combination in animal communication, with a disjunction being the combination of two or more units with at least one of the propositions being true.

Existing literature also offers some examples of call or sound combinations produced by some mongoose species that should be considered in order to gain an overview of combinatoriality in social mongooses. Meerkats have been documented to combine calls in predation contexts. They emit predator-specific alarm calls in response to terrestrial predators which they can combine with a moving-animal call, generally given to any moving animal, predatory or not, in their environment (Manser, 2009; Manser et al., 2014). These terrestrial – moving-animal call combinations are given in response to moving, and therefore potentially more dangerous, terrestrial predators and cause a stronger reaction than to either of these calls played back independently (Manser et al. unpub. data). These combinations can thus be considered as syntactic, providing information on both the type of threat and its activity. Furthermore, banded mongooses (*Mungos mungo*) have been described to combine sounds within their close calls. These close calls are composed of two segments, the first noisy segment varies consistently with the caller's identity and the second harmonic segment varies as a function of the caller's activity (Jansen et al., 2012). Banded mongoose close calls appear similar to simple syntactic combinations, resembling predicate-argument structures in human language, such as "*I dig*" (chapter 1). Banded mongooses can further combine these close calls with other calls in the context of leading the group, being lost from the group or in excitement at rain or wet ground (Jansen, 2013). However, the information receivers can extract from these close calls and their combinations has yet to be investigated (Jansen, 2013).

Implications for the Evolution of Combinatoriality in Human Language

Results from studies of combinatoriality in mongoose communication can offer some insight into the emergence of combinatoriality in human language. First it appears that the combinations resulting from the seemingly more simple mechanisms, as documented in meerkat social contexts (chapter 2), resemble neither phonology nor syntax. According to the definition of phonology, for these combinations to be phonology-like, rearranging the component calls would have to affect the meaning of the combination (McGregor, 2009). Whilst the meaning the receivers extract from these combinations has not yet been tested, most of these combinations present a fixed, stereotyped, structure (e.g. di-drrr calls) or are repetitions of the same call type (e.g. short call sequences), automatically precluding any element rearrangement. Only long sequences, with a more variable structure, would offer a possible candidate in which to investigate the existence of phonology-like combinations in meerkat

social call combinations. In accordance with the definition of syntax, for these social combinations to be syntax-like, the individual social calls would first have to have a specific meaning (de Boer et al., 2012), for which we do not currently have any evidence. Whilst the fixed structure combinations emitted by meerkats may permit an increase in the number of "objects" ("object" is used here as in Nowak et al. (1999) to define objects in the environment, other people or animals, concepts or actions) that can be communicated about, most meerkat social call combinations seem instead to reflect a sequential change in the caller's internal state. This differs from human languages whose content can be separated from the speaker's internal state; speakers can, for example, communicate about distant objects, inexistent objects or even provide false information. However, speech can convey emotional cues independently from content (Ververidis and Kotropoulos, 2006).

Combinations on both levels of duality of patterning in human language permit an increase in the number of objects that can be communicated about. However, only syntax-like combinations have so-far been documented in mongoose vocal communication, with no unambiguous examples of phonology-like sequences. This mirrors findings in other species as described in chapter 1. Thus, despite new evidence of a phonemic-contrast in chestnut-crowned babblers (*Pomatostomus ruficeps*: Engesser et al., 2015), syntax still appears to be generally more widespread in animal communication than phonology, supporting the hypothesis that syntax emerged before phonology (chapter 1).

One prerequisite for syntactical combinations is the existence of meaningful calls/words, for which there is an association between a sound and an object. These associations should evolve when an efficient transfer of information is beneficial to both the caller and the receiver (Nowak and Krakauer, 1999). This may explain why meaningful calls, and therefore the potential for syntax-like combinations, appear to be more often documented in predation contexts, in which the benefits of reliable information transfer may be higher in terms of survival for the receiver and in terms of indirect fitness for the caller if related to the receiver (Blumstein, 1999, 2007). Alternatively, there may be a bias towards describing calls in predation contexts as meaningful because, in many cases, their referents are easily discernible and they elicit very stereotyped behaviours, which contrasts with the often more subtle behavioural responses elicited by social calls. Nevertheless, syntax-like combinations are found in social contexts, as evidenced by banded mongoose close calls (Jansen et al., 2012). In this case, transfer of information about identity and activity to other group members may be important to group cohesion and therefore

survival in this social species, given that single mongooses are generally more vulnerable to predators than when part of a group (described in meerkats: Clutton-Brock et al., 1999).

Once meaningful calls are present in a species repertoire, syntax should emerge when the number of objects that require communication exceeds the number of calls in the repertoire (Nowak and Krakauer, 1999). This does not seem immediately obvious in mongooses, in particular in the case of dwarf mongoose alarm calls, where they produce eleven distinct call types despite only being threatened by a small number of predator categories. Nevertheless, it is possible that the existing calls are already used to communicate about highly specific objects in the environment or about specific aspects of these objects (e.g. as described in Gunnison's prairie dogs, *Cynomys gunnisoni*: Slobodchikoff et al., 2009) and thus call combinations become necessary to increase the number of objects the mongooses can communicate about. Alternatively, it may be cognitively simpler to combine two existing meaningful calls, for which the sound-meaning associations are already in place, into a sequence with a related meaning rather than learning a completely new sound-meaning association (Nowak and Krakauer, 1999).

Despite some similarities between comparative examples of syntax and the same phenomenon in humans, there are also some striking differences between these systems. First, there is little reuse of the same meaningful calls in different combinations in animal communication and, when elements are reused, it is rarely in more than two or three distinct combinations (e.g. in Campbell monkeys, *Cercopithecus campbelli campbelli*: Ouattara et al., 2009; banded mongooses: Jansen, 2013; pied babblers, *Turdoides bicolor*: Engesser et al., 2016). This contrasts with the generativity of human languages in which a given word can be part of a large, theoretically infinite, number of sentences. Furthermore, the reuse of the same elements in different sequences can be critical for the interpretation of combinations in animal communication, especially if one element is not produced independently, as in the case of male Campbell monkey alarm call affixation (Ouattara et al., 2009). Second, syntactic-like combinations produced by animals seem to be very limited in length, with those described in the literature being restricted to two component call types (though banded mongooses may combine three meaningful elements, this has not yet been examined in detail; Jansen, 2013). This again contrasts strongly with human languages, in which the number of words in a sentence technically has no upper limit, other than the producer and receiver's memory capacity. These two points highlight that, whilst simple syntax-like combinations are found in

the communication systems of various non-human animal species, there are still vast differences with the use of syntax in human languages.

There are also major differences between comparative examples of phonology-like call combinations in animal communication and their counterparts in human language. Models show that phonology should emerge after a linguistic error limit is reached (Nowak et al., 1999; Nowak and Krakauer, 1999). This error limit is hypothesised to be the maximum number of sounds present in a repertoire beyond which adding a new signal will lead to an increase in receiver error (Nowak et al., 1999; Nowak and Krakauer, 1999). In order to communicate about more objects, it is then more efficient to combine meaningless sounds together into meaningful words than to produce a new sound. So far, these forms of combinations have not been documented in social mongoose communication, possibly because the number of objects they need to communicate about does not exceed the number of calls present in their relatively large repertoires (15 to 30 call types: Manser et al., 2014).

Finally, by comparing the combinations produced by closely related species it may be possible to start to disentangle the influence of various factors on the emergence of combinatoriality. All three mongoose species discussed here are social, making it hard to directly investigate the impact of sociality on the production of call combinations. However, comparisons with solitary species (e.g. slender mongooses, *Galerella sanguinea*: Rood, 1989) may be difficult as such species would have little need for vocal communication in the first place. Nevertheless, a detailed investigation for call combinations in the vocal communication systems of facultative social species (e.g. yellow mongoose, *Cynictis penicillata*: Le Roux et al., 2009) could offer an interesting avenue to study the impact of sociality on combinatoriality. These combinations could further be compared with those produced by obligate social species with a more complex social structure. Contrary to sociality, the mongoose species considered here did differ in habitat preference, with meerkats living in semi-arid deserts and dwarf and banded mongooses living in more vegetated areas (Manser et al., 2014). All of these species, living in both habitats, produce call combinations, superficially indicating that habitat has little influence on the development of combinatoriality. However, to my knowledge, combinations have not yet been explored in dwarf mongoose social communication or in banded mongoose alarm calls, making any comparisons incomplete. The more combinatoriality in species of differing social structures and living in different habitats is investigated, the better understanding will be gained

of the distribution of combinatorial abilities in relation to social and environmental factors. This could ultimately help to better reconstruct the evolutionary history of combinatoriality.

Methodological Issues

Currently, comparative research into the evolution of combinatoriality presents some issues and limitations. The most obvious concern is the lack of a common definition of a combination. To date, many combinations are defined relatively subjectively. Whilst these combinations are difficult to dispute if the individual calls or sounds are concatenated with no silence between them (e.g. dwarf mongoose T_3 alarm call: chapter 4; banded mongoose close calls: Jansen, 2013), identifying combinations this way is more problematic when the individual elements are separated by a period of silence (e.g. meerkat short calls: chapter 2). More objectively, mathematical algorithms can be used to analyse sequences (Kershenbaum et al., 2014). However, these still do not take into account what the animals themselves perceive as a combination as opposed to individual calls. One potential solution is to employ perception experiments in which the component calls of the combination are separated by increasing lengths of silence. The inter-call silence duration above which the subjects' response resembles sequential reactions to the individual calls rather than a reaction to the call combination could then, theoretically, be determined.

Another concern is how to ascertain that a combination is indeed a combination of two independent calls and not simply constituted of structurally similar but different calls. Some studies have used acoustic analyses to determine whether individual and component calls are statistically the same (e.g. Engesser et al., 2016; chapter 4), however this again does not consider how the animals themselves perceive the combination. In order to do this, it is possible to carry out playbacks of artificial combinations created from individual calls. If responses to these artificial combinations are comparable to responses given to naturally produced combinations, then it can be assumed that the subjects do in fact perceive the sequence as a combination of individual calls. Moreover, performing playbacks of the artificially isolated components of the combination, as done in chapter 4, can further confirm the combinatorial nature of the sequence if they evoke a similar response to those given when exposed to the individual calls.

An additional issue is how to determine if a combination is phonology-like. One of the main tools to determine phonology in human languages is the minimal pair approach, in which pairs of words are searched for where a change in one phoneme changes the meaning of the word (Yip, 2006). Thus, when searching for phonology-like combinations in animal communications, one should look for two combinations with different meanings or functions that differ only by one element. To date, a change in meaning associated with the change of only one element in the sequence has been demonstrated in just one species, the chestnut crowned babbler (Engesser et al., 2015).

Determining if a combination is syntax-like can also be complex. First, the individual component calls of a syntactical combination need to have meaning. In animal communication, this most often involves functionally referential calls. These calls are given to a specific external stimulus and cause an adaptive behavioural response in receivers, even in the absence of the eliciting stimulus (Macedonia and Evans, 1993). However, many calls in animal communication can convey context-specific information such as caller's identity for example (Shapiro, 2010), which could also be considered as having meaning, despite not referring to an external object or event.

Furthermore, for a combination of meaningful calls to be considered syntax-like, the meaning of the combination must be related to the meanings of its parts. One way to establish this is to determine the meaning of the individual calls and of the combination and ascertain if there is overlap or similarity between them. This can be done by studying the subjects' responses to these calls and combinations through observations and, ideally, playback experiments. Nevertheless, receivers' responses to call combinations may be the result of simpler mechanisms than syntactic-like processing of the combination. Certain control playback experiments can be used to rule out some of these mechanisms. For example, a stimulus composed of two calls may simply be more salient than a stimulus composed of a single call and therefore evoke a stronger response (Engesser et al., 2016). This can be controlled for by either playing back a repetition of the same individual call or an artificial combination with a different, neutral, call from the species repertoire. If the subjects show a weaker response compared to that produced when hearing the combination, stimulus saliency can be ruled out.

Finally, it is sometimes debated whether the order of component calls within a sequence needs to influence the meaning of the combination in order for the latter to be defined as syntax-like. However, in many human languages the order of the words in a sentence is not essential to

understanding the sentence's meaning, though in these cases the relationships between words are often encoded with grammatical markers instead (Kaiser and Trueswell, 2004). It would therefore seem that the influence of call order on combination meaning should not be pivotal to determining if a combination is syntax-like or not.

Conclusions and Outlook

In conclusion, this thesis has taken an explicitly comparative approach to language evolution research, with a particular focus on the emergence of combinatoriality. A multidisciplinary approach has provided new insights on existing examples of combinatoriality in animal communication described in the literature. From an experimental perspective, this thesis has built on previous studies in social mongooses, showing that meerkats use a large variety of combinations of various structures in different social settings and that dwarf mongooses produce disjunction-like combinations of meaningful alarm calls. However, some aspects of combinatoriality in social mongooses are yet to be explored. In particular it would be interesting to determine whether dwarf mongooses also produce call combinations in social situations, and if that is the case, what form these combinations take. Such research would build on previous studies on social call combinations in meerkats and banded mongooses as well as facilitating a comparison between social and predation contexts, potentially offering insights into their respective influence on the emergence of combinatoriality.

REFERENCES

Blumstein, D.T., 2007. The evolution, function, and meaning of marmot alarm communication. Adv. Study Behav. 37, 371–401.

Blumstein, D.T., 1999. The evolution of functionally referential alarm communication: Multiple adaptations; multiple constraints. Evol. Commun. 3, 135–147. doi:10.1075/eoc.3.2.03blu

Clutton-Brock, T.H., Gaynor, D., McIlrath, G.M., Maccoll, A.D.C., Kansky, R., Chadwick, P., Manser, M.B., Skinner, J.D., Brotherton, P.N.M., 1999. Predation, group size and mortality in a cooperative mongoose, *Suricata suricatta*. J. Anim. Ecol. 68, 672–683.

de Boer, B., Sandler, W., Kirby, S., 2012. New perspectives on duality of patterning: Introduction to the special issue. Lang. Cogn. 4, 251–259. doi:10.1515/langcog-2012-0014

Engesser, S., Crane, J.M.S., Savage, J.L., Russell, A.F., Townsend, S.W., 2015. Experimental Evidence for Phonemic Contrasts in a Nonhuman Vocal System. PLOS Biol. 13, e1002171. doi:10.1371/journal.pbio.1002171

Engesser, S., Ridley, A.R., Townsend, S.W., 2016. Meaningful call combinations and compositional processing in the southern pied babbler. Proc. Natl. Acad. Sci. 201600970.

Jansen, D.A.W.A.M., 2013. Vocal communication in the banded mongoose (PhD). University of Zurich, Zurich, Switzerland.

Jansen, D.A.W.A.M., Cant, M.A., Manser, M.B., 2012. Segmental concatenation of individual signatures and context cues in banded mongoose (*Mungos mungo*) close calls. BMC Biol. 10, 97. doi:10.1186/1741-7007-10-97

Kaiser, E., Trueswell, J.C., 2004. The role of discourse context in the processing of a flexible word-order language. Cognition 94, 113–147.

Kershenbaum, A., Blumstein, D.T., Roch, M.A., Akçay, Ç., Backus, G., Bee, M.A., Bohn, K., Cao, Y., Carter, G., Cäsar, C., Coen, M., DeRuiter, S.L., Doyle, L., Edelman, S., Ferrer-i-Cancho, R., Freeberg, T.M., Garland, E.C., Gustison, M., Harley, H.E., Huetz, C., Hughes, M., Hyland Bruno, J., Ilany, A., Jin, D.Z., Johnson, M., Ju, C., Karnowski, J., Lohr, B., Manser, M.B., McCowan, B., Mercado III, E., Narins, P.M., Piel, A., Rice, M., Salmi, R., Sasahara, K., Sayigh, L., Shiu, Y., Taylor, C., Vallejo, E.E., Waller, S., Zamora-Gutierrez, V., 2014. Acoustic sequences in non-human animals: a tutorial review and prospectus. Biol. Rev. doi:10.1111/brv.12160

Le Roux, A., Cherry, M.I., Manser, M.B., 2009. The vocal repertoire in a solitary foraging carnivore, *Cynictis penicillata*, may reflect facultative sociality. Naturwissenschaften 96, 575–584.

Macedonia, J.M., Evans, C.S., 1993. Essay on contemporary issues in ethology: Variation among mammalian alarm call systems and the problem of meaning in animal signals. Ethology 93, 177–197. doi:10.1111/j.1439-0310.1993.tb00988.x

Manser, M.B., 2009. What Do Functionally Referential Alarm Calls Refer To?, in: Cognitive Ecology II. University of Chicago Press, Chicago, IL, USA, pp. 229–246.

Manser, M.B., Jansen, D.A.W.A.M., Graw, B., Hollén, L.I., Bousquet, C.A.H., Furrer, R.D., le Roux, A., 2014. Vocal complexity in meerkats and other mongoose species, in: Advances in the Study of Behavior. Elsevier, pp. 281–310.

McGregor, W.B., 2009. Linguistics: An Introduction. Continuum, London, UK.

Nowak, M.A., Krakauer, D.C., 1999. The evolution of language. Proc. Natl. Acad. Sci. 96, 8028–8033. doi:10.1073/pnas.96.14.8028

Nowak, M.A., Krakauer, D.C., Dress, A., 1999. An error limit for the evolution of language. Proc. R. Soc. Lond. B Biol. Sci. 266, 2131–2136. doi:10.1098/rspb.1999.0898

Ouattara, K., Lemasson, A., Zuberbühler, K., 2009. Campbell's monkeys use affixation to alter call meaning. PloS One 4, e7808. doi:10.1371/ journal.pone.0007808

Rood, J.P., 1989. Male associations in a solitary mongoose. Anim. Behav. 38, 725–728. doi:10.1016/S0003-3472(89)80024-7

Shapiro, A.D., 2010. Recognition of individuals within the social group: signature vocalizations, in: Brudzynski, S.M. (Ed.), Handbook of Behavioral Neuroscience, Handbook of Mammalian VocalizationAn Integrative Neuroscience Approach. Elsevier, pp. 495–503.

Slobodchikoff, C.N., Paseka, A., Verdolin, J.L., 2009. Prairie dog alarm calls encode labels about predator colors. Anim. Cogn. 12, 435–439. doi:10.1007/s10071-008-0203-y

Suzuki, T.N., Wheatcroft, D., Griesser, M., 2016. Experimental evidence for compositional syntax in bird calls. Nat. Commun. 7, 10986. doi:10.1038/ncomms10986

Ververidis, D., Kotropoulos, C., 2006. Emotional speech recognition: Resources, features, and methods. Speech Commun. 48, 1162–1181. doi:10.1016/j.specom.2006.04.003

Yip, M.J., 2006. The search for phonology in other species. Trends Cogn. Sci. 10, 442–446.

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2007: **Baccalauréat** Scientifique, Lycée Desfontaines, Melle, France

2010: **Bachelor's degree** "Biologie des Organismes", Université Rennes I, France

2011: **Master's degree 1st year** "Comportement Animal et Humain", Université Rennes I, France

Thesis: Effect of noise on domestic canary (*Serinus canaria*) song
Supervisor: Tudor Draganoiu
Laboratory: L.E.C.C., Université Paris X, Nanterre, France

2012: **Master's degree 2nd year** "Comportement Animal et Humain", Université Rennes I, France

Thesis: Effect of age on European starling (*Sturnus vulgaris*) song
Supervisors: Isabelle George, Laurence Henri, Hugo Cousillas & Martine Hausberger
Laboratory: Ethos, Université Rennes I, France

2016: **Doctoral studies**, University of Zurich, Switzerland
Thesis: Social mongoose vocal communication: insights into the emergence of linguistic combinatoriality
Supervisors: Simon W. Townsend, Marta B. Manser, Balthasar Bickel, Carel P. van Schaik
Laboratory: Animal Behaviour group, Department of Evolutionary Biology and Environmental Studies, University of Zurich, Switzerland

Publications

Collier K., Bickel B., van Schaik C.P., Manser M.B. & Townsend S.W., 2014. Language evolution: syntax before phonology? Proceedings of the Royal Society B: Biological Sciences 281.

Collier K., Townsend S.W. & Manser M.B., accepted. Call concatenation in wild meerkats. Animal Behaviour.

In preparation:

Collier K., Radford A. N., Townsend S. W. & Manser M. B., in prep. Wild dwarf mongooses produce both urgency related and predator-specific alarm calls.

Collier K., Radford A. N., Stoll S., Manser M. B., Bickel B. & Townsend S.W., in prep. Meaningful call combinations in the alarm call system of dwarf mongooses (*Helogale parvula*): evidence for disjunction?

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BIO 554: Topics in evolutionary biology……1 ECTS

Methods

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Subject specific matter

Wahlpflichtveranstaltung 1…….4 ECTS

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